THE COMPARATIVE AND FUNCTIONAL CRANIAL MORPHOLOGY OF THE EARLY THEROCEPHALIA (AMNIOTA : THERAPSIDA)

by

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VERKLARING

Ek die ondergetekende verklaar hiermee dat die werk in hierdie proefskrif vervat, my eie oorspronklike werk is wat nog nie vantevore in die geheel of gedeeltelik by enige ander Universiteit ter verkryging van 'n graad voorgelê is nie.

7/8/1988
Datum

vir

Lorna, Lizét en Martine

Diep in my gesteente berg ek hul gebeente -
die geheim van hul lewe en lot

Die Vlakte, Jan F.E. Celliers

MORTUI VIVOS DOCENT

UITTREKSEL

Die skedelmorfologie van die vroeë Therocephalia word bespreek op historiese, anatomies-vergelykende en taksonomiese grondslag. Daar word aangetoon dat die familienaam Scylacosauridae voorrang geniet bo die algemeen aanvaarde naam Pristerognathidae en dat ander historiese familiename binne die Therocephalia, te wete Alopecodontidae en Ictidosauridae ongeldig is en gevolglik binne die parameters van die enkele familie Scylacosauridae resorteer.

Nuwe eksemplare het ook aan die lig gebring dat 'n digotomie binne die vroeë Therocephalia bestaan en dat 'n tweede takson, gebaseer op 'n groot aantal anatomiese kenmerke, gevolglik uitgeken kan word. Die familienaam Lycosuchidae is beskikbaar vir hierdie takson.

Al die geldige taksa wat voorheen in die Pristerognathidae, Lycosuchidae, Alopecodontidae en Ictidosauridae gegroepeer is, resorteer dus binne hierdie twee groepe. 'n Groot aantal taksa bestaan in die literatuur as gevolg van swak gepreserveerde eksemplare wat verkeerd geïdentifiseer is. 'n Besondere poging is dus aangewend om al die eksemplare op 'n meer objektiewe grondslag te beoordeel. As gevolg hiervan het die aantal geldige taksa drasties afgeneem. Die Lycosuchidae word verteenwoordig deur die

enkele takson Lycosuchus en die Scylacosauridae deur Scylacosaurus, Pristerognathus, Pardosuchus, Ictidosaurus, Glanosuchus en Alopecodon.

Kladistiese analise van die afkomskenmerke toon dat die Scylacosauridae nader verwant aan die res van die Therocephalia is as aan die Lycosuchidae. Die Lycosuchidae word dus beskou as die sustergroep van die Scylacosauridae + die res van die Therocephalia.

Numeriese en alfabetiese lyste van al die eksemplare wat ooit in die bostaande families geplaas is, word verskaf. Elke eksemplaar word uitvoerig bespreek en fotografies gedokumenteer met behulp van stereofotos in 'n poging om die evaluering daarvan so objektief as moontlik te maak en om die leser wat nie die eksemplare eerstehands kon inspekteer nie, te help.

Sleutelwoorde:
Vergelykende skedelmorfologie, taksonomie, Synapsida, Therapsida, Theriodontia, Therocephalia, Scylacosauridae, Lycosuchidae, Pristerognathidae, Perm, Karoo Supergroep, Beaufort Groep, Tapinocephalus-sone.

ABSTRACT

The cranial morphology of the early Therocephalia is discussed on a historical, comparative and a taxonomic basis. It is shown that the family name Scylacosauridae has precedence over the generally used name Pristerognathidae and that other historical therocephalian family names viz. Alopecodontidae and Ictidosauridae fall within the parametres of the Scylacosauridae and are consequently invalid.

In addition, new material has shown that a dichotomy exists within the early Therocephalia and a second taxon, based on a large number of anatomical features, can consequently be identified. The family name Lycosuchidae is available for this taxon.

Into these two groups are incorporated all the valid taxa previously placed in the Pristerognathidae, Lycosuchidae, Alopecodontidae and Ictidosauridae. Because a large number of taxa exist in the literature as the result of poor specimens wrongly identified, a particular attempt was made to assess all the material on a more objective basis. As a result the number of valid taxa has been drastically reduced. The Lycosuchidae is represented by the single taxon Lycosuchus and the Scylacosauridae by Scylacosaurus, Pristerognathus, Pardosuchus, Ictidosaurus, Glanosuchus and Alopecodon.

Cladistic analysis of the derived characters indicate

that the Scylacosauridae is more closely related to the rest of the Therocephalia than to the Lycosuchidae. The Lycosuchidae is therefore the sister group of the Scylacosauridae + rest of the Therocephalia.

Numerical and alphabetical lists of all specimens ever included in the above families are supplied. Each specimen is extensively discussed and photographically documented by means of stereo photographs in an effort to increase the objectivity of the assessment and to assist those readers whom may not have had the oppurtunity to inspect all the specimens at first hand.

Key Words:
Comparitive skull morphology, taxonomy, Synapsida, Therapsida, Theriodontia, Therocephalia, Scylacosauridae, Lycosuchidae, Pristerognathidae, Permian, Karoo Supergroup, Beaufort Group, Tapinocephalus Zone.

Резюме

Черепная морфология ранних тероцефалов рассматривается на историческом, сравнительном и таксономическом основании. Указывается на то, что родовое название Scylacosauridae более предпочительно, чем широко употредляемое название Pristerognathidae и что другие исторические тероцефальные родовые названия, такие как Alopecodontidae и Ictidosauridae должны быть включены в общий род Scylacosauridae и следовательно недействительные.

К тому же, новый материал показал что у ранних тероцефалов существует дихотомия и что второй таксон следовательно может отождествить основан на большом количестве анатомических характеристик. Родовое название Lycosuchidae для этого таксона доступное.

В эти две группы включаются все существующие таксоны, которые были прежде включены в группы Pristerognathidae, Lycosuchidae, Alopecodontidae, и Ictidosauridae. Так как в литературе существует большое количество таксонов в результате убогих экземпляров неправилыно определены, в частности сделана попытка определить весь материал на более объективном основании. В результате этого количество действительных таксонов круто редуцировалось. Lycosuchidae представлает единственным таксоном *Lycosuchus*, а Scylacosauridae : *Scylacosaurus*, *Pristerognathus*, *Pardosuchus*, *Ictidosaurus*, *Glanosuchus* и *Alopecodon*.

Кладистический анализ происходяших характеров указывает что Scylacosauridae более близко родствен с остальными тероцефалами чем с Lycosuchidae. Lycosuchidae следовательно сестринская группа Scylacosauridae и остальных Therocephalia.

Дается числовой и алфавитный перечень всех экземпляров, которые были поныне включены в выше-названные роды. Каждый отдельный экземпляр исчерпывающе обсужден и проиллюстрирован стерео-фотографиями с цельню повышения степени объективности оценки и помощи читателю, у которого не было возможности осмотреть

все экземпляры.

CONTENTS

1. INTRODUCTION

In an evolutionary sense the Synapsida is the most important body of fossils in the entire spectrum of past life encompassed by the terrestrial fossil record. One of the reasons for this is that their fossil record supplies the most complete evidence yet known of the origin of one major taxon from another viz. mammals from reptiles. Within the Synapsida the Therapsida occupy a central position because of their relative abundance and the completeness of their fossil record. Their real importance, however, lies in the fact that morphologically they occupy an intermediate position between the pelycosaurs and the mammals and that the pattern of morphological change demonstrated within the group uniquely documents the gradual development of mammals from reptiles.

It is currently accepted that within the Therapsida the phylogenetic line leading to cynodonts and thus also to mammals is reflected in the cranial morphology of the Therocephalia rather than the Gorgonopsia, although in isolated cases recent authors i.e. McLoughlin (1980) still adhere to the now discredited view of Watson (1921) who favoured a gorgonopsid-like precursor for the Cynodontia. The interrelationships of the various therocephalian taxa are therefore an important link in the evolutionary pathway culminating in the origin of mammals.

The Therocephalia occur most abundantly in the strata of the Beaufort Group of Southern Africa although a small number of forms have been recorded from elsewhere. Outside Africa the only therocephalian finds of note have been in Antarctica, USSR and China. Colbert and Kitching (1981) recorded fragmentary specimens of Ericiolacerta, Pedaeosaurus, and Rhigosaurus, together with a small unidentified therocephalian maxilla and associated dentary, from the Lower Triassic Fremouw Formation of Antarctica. Young (1952) described the Upper Permian Urumchia lii from the banks of the Urumchi river, Sinkiang, Peoples Republic of China. A number of therocephalians have been recorded from the Upper Permian Tatarian Substage, Lower Triassic Vetluzhskaya Series and Middle Triassic Donguzskaya Formation of the USSR viz. Moschowhaitsia (Tatarinov 1963), Scylacosuchus (Tatarinov 1968), Chthonosaurus (Vjuschkov 1955), Hexacynodon (Tatarinov 1974), Annatherapsidus (Kuhn 1961), Porosteognathus (Vjuschkov 1955), Scalopognathus (Tatarinov 1974), Nothógomphodon (Tatarinov 1974) and Dongusaurus (Vjuschkov 1964). In addition Tatarinov (1982) reported the discovery of skull remains of a new large Upper Triassic therocephalian.

Within Africa the Therocephalia have, with few exceptions, been almost exclusively recorded from the Beaufort sediments of the South African Karoo. Boonstra (1953b) briefly mentioned two weathered snouts collected by G. M. Stockley from the Ruhuhu Coalfield Region of Tanzania. He regarded one as a probable therocephalian and the other as a

form more advanced than the early Therocephalia of the South African Tapinocephalus zone. Drysdall and Kitching (1963) mentioned a single specimen resembling Pristerognathus from the lower fossiliferous beds of the Madumabisa Mudstone in the Upper Luangwa Valley of Zambia. Four other specimens are mentioned from localities in the upper fossiliferous beds of the Madumabisa Mudstone but they appear not to belong to the early Therocephalia since they are associated with taxa which in the South African context typify the Daptocephalus (then Cistecephalus) zone.

According to Boonstra (1969b), the Busi Valley, Zimbabwe has also yielded therocephalian remains. This find by A.M. Macgregor consisted mianly of a number of badly weathered dinocephalian fragments of Tapinocephalus-Zone age. These specimens were briefly described by Boonstra (1946) but thought too inadequate to be named. Boonstra did, however, mention the presence of limb bones and dorsal vertebrae comparable in size to that of a medium-sized therocephalian or gorgonopsian. Later, (1969b) he positively identified these remains as therocephalian, probably pristerognathid. In addition Keyser and Brink (1979) recorded a skull of the bauriid Herpetogale marsupialis from the Middle Triassic Anisian Omigonde Formation of South West Africa/Namibia. The badly weathered snout from the Ruhuhu valley, Tanzania, described by Parrington (1936b) as a possible therocephalian, is most likely a gorgonopsian as the canines are too large for it to be an advanced therocephalian and the vomers appear to

be too wide anteriorly to be an early therocephalian. Parrington eventually realised that his identification was in doubt as is shown by a footnote in the paper of Kermack (1956 p.125) where the author mentions that Parrington informed him in 1953 that the specimen could equally well be a gorgonopsian.

Within the Beaufort sediments the Therocephalia occur from the base of the Upper Permian Tapinocephalus Zone (Dinocephalian and Pristerognathus/Diictodon Assemblage Zones of Keyser and Smith 1979) to the Lower Triassic Cynognathus Zone (Kannemeyeria Assemblage Zone of Keyser and Smith 1979). For the purpose of this investigation the zone terminology of Kitching (1977) will be employed. Within this time span of approximately 50 Ma they exhibit marked morphological changes, especially in skull structure, which progressively attain a mammalian character. In addition, recent finds (Rubidge, Kitching and Van den Heever, 1983) have recorded the first early therocephalian ever documented from formations below that of the Tapinocephalus Zone. Whilst this initial find in Ecca Group strata consists of only two partial skulls recovered from approximately 200m below what is currently regarded as the base of the Tapinocephalus Zone, the dicynodont fauna is already wel represented from this area by more than 30 skulls, of which a number have been referred to the primitive Eodicynodon by Barry (1974, 1975) and Rubidge (1983). In addition the partial skulls of 5 large dinocephalians, one gorgonopsian and one small possible

dromasaur have also been recovered by Rubidge (1983, and pers. comm.) from the same stratigraphic level.

Other earlier finds from allegedly Ecca Group strata include the two fragmentary dinocephalians Eccasaurus priscus SAM 915 and Titanosuchus (Archaeosuchus cairncrossi) SAM 916 as well as the therocephalian Karoowalteria skinneri BPI 220. Boonstra (1955) identified the humerus of Eccasaurus as that of an anteosaurid and the associated incisor as that of a tapinocephalid, and not a therocephalian as reported by Barry (1972). Later, Boonstra (1969b) stated that the two dinocephalians were in fact recovered from the Tapinocephalus Zone. Rossouw (1955) established that Karoowalteria, initially assigned to the Ecca by Brink and Kitching (1951) was in fact recovered from Elandsfontein 257, Beaufort West in the Tapinocephalus Zone. (See Barry (1972) and Rubidge (1983) for a complete list of specimens purported to be from Ecca Group strata.)

Therocephalians typically possess the following: a narrow intertemporal region, large, dorsally facing temporal fenestrae, suborbital fenestrae in the palate (secondarily closed in some whaitsiids), various developmental stages of the secondary palate, a stapes which lacks a stapedial foramen, an unfused jaw symphysis, a thin, plate-like splenial, a posteriorly sloping mentum, an anteroposteriorly widened epipterygoid; a vomer which contacts the pterygoid in the ventral midline of the palate and a palatine devoid of teeth. According to Hopson and Barghusen (1986) the squamosal

is emarginated ventrally to expose much of the quadratojugal in lateral view, as in cynodonts. There is some doubt as to whether this feature is restricted to cynodonts and therocephalians since it may also be present in certain gorgonopsians i.e. Lycaenops (Tanqaqorgon) tenuirostris SAM 11744 (see also Sigogneau 1970).

The Therocephalia may be conveniently grouped into a number of easily recognisable taxa. The early Therocephalia (Alopecodontidae, Ictidosauridae, Lycosuchidae, Pristerognathidae, Scylacosauridae) are large primitive Tapinocephalus Zone carnivores. Within this group the Pristerognathidae is the most abundant and has in time come to be regarded as representative of the early Therocephalia. In addition Van den Heever (1980) suggested that the family Lycosuchidae was invalid and should therefore be included in the Pristerognathidae.

The Whaitsiidae are fairly large Daptocephalus Zone forms lacking both upper and lower postcanine teeth and suborbital fenestrae (Moschowhaitsia is an exception) but possessing a specialised rudimentary secondary palate. The Akidnognathidae (=Annatherapsidae, Euchambersiidae, Moschorhinidae) comprises smaller forms lacking a secondary palate but possessing anteriorly widened vomers. The latter occur from the Cistecephalus Zone (Euchambersia only) through the Daptocephalus Zone to the Lystrosaurus Zone. The remaining therocephalian taxa comprise a series of predominantly Daptocephalus and Lystrosaurus Zone families, a major feature

of which is the gradual development of a secondary palate. They have been variously grouped as the infraorder Bauriamorpha by Watson and Romer (1956), or the infraorder Scaloposauria by Brink (1965). This arrangement has been criticised by Kemp (1982), who doubts that they form a monophyletic group with regard to the rest of the Therocephalia, and Hopson and Barghusen (1986), who regard the Bauriamorpha and Scaloposauria together as a subgroup of the Therocephalia, the Baurioidea. They point out that usage of the term Scaloposauria as a taxonomic unit should be discontinued since it is based on juvenile individuals of species which are not all baurioids. According to Hopson and Barghusen (1986) the Baurioidea consists of a number of families each of which is typified by one of the following taxa; Ictidosuchoides, Ictidosuchops, Regisaurus, Lycideops, Ericiolacerta and Bauria. One new family, the Hofmeyriidae, is advocated by them to include the small Cistecephalus Zone forms Hofmeyria (= possibly Mirotenthes) and Ictidostoma. Two additional Tapinocephalus Zone specimens which are of uncertain affinity are Crapartinella croucheri and Simorhinella baini. Mendrez (1975a) placed the former in the Crapartinellidae and the latter in the Simorhinellidae.

In spite of the phylogenetic affinity of the Therocephalia to the Cynodontia and the Mammalia there still does not exist a functional systematic framework within the group pinpointing the proximity of the various taxa to each other. This has clouded the relationships amongst the members

of the group as well as between the Therocephalia and other members of the Therapsida.

The Therocephalia from the Tapinocephalus Zone are generally poorly preserved, most often distorted and almost always incomplete. In conjunction with the almost intractable matrix these conditions must at times have daunted even the most ardent preparators. Consequently these taxa have received relatively scant attention in the antomical literature over the past 50 years. The resulting lack of detailed information is demonstrated by Kemp (1982) in his book on the mammal-like reptiles in which the Pristerognathidae, representing the early Therocephalia, is disposed of in a single paragraph.

Because of this situation the systematic placement of new specimens as well as the reassessment of existing material has often been hampered, resulting in a taxonomic quagmire where invalid species have existed in the literature for many years, confusing relationships.

An attempt has therefore been made here to study all specimens relevant to the project at first hand and to assess both the preservation and the amount of distortion present. Since most of the specimens are distorted in some way or another the danger inherent in basing descriptions on single specimens are immediately apparent. For taxonomic purposes it is therefore essential that the widest possible variety of comparative material should be investigated. It is also of cardinal importance that comparative descriptions of taxa

should not only be based on previous descriptions or illustrations unless absolutely necessary, but rather on the first hand inspection of the material where possible. The danger of relying on previous authors who may not have inspected the material at first hand has been amply illustrated in the literature. A case in point is that of Scylacoides ferox AMNH 5558 which is, as Boonstra (1935a) correctly pointed out, so poor that it is not possible to determine with certainty even the suborder to which it belongs. Subsequent authors viz. Von Huene (1938), Romer (1945), Haughton and Brink (1955), Von Huene (1956), Romer (1956), Watson and Romer (1956), Vjuschkov (1964) and Romer (1966) all ignored Boonstra's (1935a) first-hand description, and followed Haughton (1924) who regarded the specimen as a member of the Pristerognathidae.

Independent interpretations of the phylogenetic position of the Therocephalia and their relationships with the Cynodontia have produced a variety of conclusions. Brink (1951) favoured forms such as Silphedestes as intermediates between cynodonts and therocephalians. Romer (1968) pointed out that he and Watson (Watson and Romer, 1956) did not accept this premise because the known members of this group were too specialised in some aspects and at that time still too incompletely known. Boonstra (1953a) regarded the Ictidosuchidae as forming the connecting link between the Pristerognathidae and the Cynodontia. Brink (1960) described Scalopocynodon as a member of the silphedestid-scaloposaurid

group and regarded it as a form ancestral to the Cynodontia. Scalopocynodon and Silphedestes are, however, now regarded as primitive cynodonts and are grouped by Hopson and Kitching (1972) with Procynosuchus. Kemp (1972a) proposed that the whaitsiids, although not the direct ancestors, lie closest of all therocephalian groups to the ancestry of the cynodonts. Gaffney (1980) accepted this view, but this novel interpretation becomes untenable when all the relevant material is examined. Hopson and Barghusen (1986) pointed out that the supposed synapomorphies between whaitsiids and cynodonts are best interpreted as primitive retentions from the pre-therocephalian common ancestor or as convergences. They regard the Therocephalia and Cynodontia as sister groups and place these taxa as the Eutheriodontia within the monophyletic Theriodontia. According to Colbert and Kitching (1981) the Scaloposauridae were probably independently derived from early Permian sphenacodonts, thereby implying a polyphyletic origin for therapsids.

The acquisition of progressively mammalian features is clearly demonstrated amongst the later Therocephalia. It is therefore necessary, irrespective of which therapsid taxon may eventually be revealed as the cynodont precursor, to elucidate the conditions within the early therocephalians in order to establish whether the adaptations of the later taxa are foreshadowed in the morphology of the earlier forms.

Because the anatomy of the earlier forms is generally less well known, their affinities with the rest of the

Therocephalia are as yet uncertain and their taxonomic position has consequently been regarded as fairly remote with respect to the rest of the Eutheriodontia (Hopson and Barghusen 1986). It is therefore important to clarify the relationships between the various therocephalian groups and especially those of the earlier forms. Hopefully such an exercise will be useful in determining with more certainty the phylogenetic proximity of each group to the evolutionary mainstream leading to mammals.

This study deals exclusively with the early Therocephalia (=Pristerognathidae) which, for the past 80 years, have been recognised as encompassing the most primitive level of therocephalian evolution amongst the South African forms. They are medium to large, strongly carnivorous, Upper Permian Therocephalia which lie close to the base of the therocephalian radiation in the Karoo. They are easily distinguished from other therocephalian taxa by their generally larger size, serrated teeth, 3 lower incisors, large canines, narrow unfused vomers and the presence of a well developed postfrontal.

Because of their phylogenetic position the early therocephalians can be important in elucidating not only the early phylogeny of the Therocephalia but may hopefully also contribute to a better understanding of the relationships between therocephalians from South Africa and the USSR. The exact systematic position of the therocephalians from the USSR in relation to those found in South Africa is not clear at

present because of a paucity and poor preservation of material from the USSR. The general consensus is that these forms are more primitive than their South African counterparts (Boonstra 1969a,b). This is borne out by specimens such as Moschowhaitsia vjuschkovi which is clearly a whaitsiid but still possesses postcanine teeth and suborbital fenestrae, as opposed to the known South African whaitsiids which lack these features.

Porosteognathus efremovi is too fragmentary for extensive comparison but it appears to be a pristerognathid by virtue of the fact that it possesses 6 upper incisors and tooth serrations. However, on the available evidence it cannot be shown that Porosteognathus efremovi is more primitive than any of the South African forms.

Scylacosuchus orenburgensis appears to be a therocephalian because of the large number of upper incisors and the apparently narrow intertemporal region. The large number of lower incisors and lack of tooth serrations however exclude it from the early Therocephalia. According to Tatarinov (1974) a small postfrontal is present and it is possible therefore that it may belong to a closely related taxon.

Chthonosaurus velocidens, which lack both a postfrontal and tooth serrations, cannot be placed within the early Therocephalia.

Hexacynodon purlinensis is a very incomplete specimen consisting only of a maxillary with the canine root and 5

additional teeth. The lack of tooth serrations effectively debars it from the early Therocephalia.

Annatherapsidus petri is difficult to evaluate from the literature. According to the diagnosis of Tatarinov (1974 p 124) the teeth possess serrated posterior edges. However, in the descriptive account (p 134) it is stated that the teeth are not serrated. The specimen apparently possesses the anteriorly widened vomers of the Akidnognathidae and would therefore be expected not to possess serrated teeth. Both Amalitsky (1927) and Tatarinov (1974) figured the specimen with the prefrontal and postfrontal excluding the frontal from the dorsal orbital margin. This condition is not characteristic of the Therocephalia as the lateral process of the frontal usually forms the dorsomedial portion of the orbital margin. In taxa where the postfrontal is still present e.g. the early Therocephalia, it is separated from the prefrontal by the lateral process of the frontal. In whaitsiids the frontal is sometimes excluded from the dorsal margin of the orbit but since a postfrontal is lacking in these forms the dorsal margin of the orbit is formed by the prefrontal and the postorbital. This arrangement is also found in cynodonts and the condition in Annatherapsidus therefore requires clarification.

The cusped postcanines of Scalopognathus exclude it from the early Therocephalia, while Nothogomphodon and the fragmentary Dongusaurus are placed among the bauriamorphs by Tatarinov (1974).

From the above it is abundantly clear that detailed information on therocephalian relationships is patently overdue. As the early Therocephalia lie closest to the base of the therocephalian radiation during the Upper Permian in the South African Karoo and, apart from the contribution of Boonstra (1954a), have not been studied in detail for the past 50 years, they are an appropriate group to commence with. This investigation is therefore an attempt to clarify the position of the various members of the early Therocephalia historically, functionally and systematically in an effort to unravel their relationships with one another. This exercise will hopefully assist in understanding their relationships with the rest of the Therocephalia.

2. HISTORICAL OVERVIEW

Historically a plethora of taxa have been included within the Pristerognathidae, a number of which have, either as a result of poor preservation or the description of non-diagnostic material, served not only to obscure the taxonomy of the group, but also its systematic position within the Synapsida. It must be admitted, however that owing to the extreme hardness of the matrix from the lower Beaufort, preparation is singularly difficult and completely prepared specimens are rare even at the present time. In an effort to define the parameters of the group on a more practical basis it is therefore necessary to review the historical development of pristerognathid systematics.

As early Therocephalia, the Pristerognathidae are all carnivorous and are consequently included with the later or advanced therocephalians, the Gorgonopsia and the Cynodontia in the sub-order Theriodontia. Because the Therocephalia is allied to the Gorgonopsia and the Cynodontia and since initial classifications combined taxa of all three groups, it will be in the interest of clarity to review the Pristerognathidae historically against a slightly broader background, commencing with the establishment of the Theriodontia as a group. The composition of the Theriodontia has, however, undergone a number of changes since its inception.

The first published account of a theriodont from the

South African Karoo was that of Galesaurus planiceps Owen (1860). Owen (1861) attempted the first classification of Permo-Triassic vertebrates from South Africa and divided the Order Anomodontia into three families: the Dicynodontia, the Cryptodontia and the Cynodontia. Galesaurus planiceps was taken as the type of the Cynodontia. Later (1876a) he extended this classification to include 3 Orders viz. Dinosauria, Theriodontia and Anomodontia. The Order Theriodontia apparently superseded the Cynodontia and was proposed for certain cold-blooded, air breathing vertebrates with a dentition similar to that of mammals. They were characterised by a carnivorous dentition in which the incisors are separated from the postcanines by a large laniariform canine in both the upper and lower jaw, with the lower canine crossing in front of the upper as in the mammals.

Initially the condition of the external nares served to subdivide the Theriodontia into 3 families: the Mononarialia, the Binarialia, and the Tectinarialia. The Mononarialia was identified by a single median naris situated terminally and by more than 3 incisors in each premaxilla. Included in this group was the scaloposaurid therocephalian Scaloposaurus constrictus. The Binarialia included forms in which a narrow premaxilla-nasal septum divides the external nares as in dinosaurs and other reptiles, and by the compressed nature of the skulls. In the Tectinarialia, typified by Gorgonops torvus, the nostrils are small in relation to the size of the skull, divided by a broader interspace of bone and roofed by

relatively thick bone, hence the name.

The Order Anomodontia was divided into the families Bidentalia, Cryptodontia, and Endothiodontia. Interestingly enough, the Cryptodontia included the badly weathered skull of the whaitsiid therocephalian Theriognathus microps, later regarded by Mendrez (1975a) as the senior synonym of the whaitsiids Alopecopsis, Aneugomphius, Hyenosaurus, Notaelurops, Notosollasia and Whaitsia. In a second paper Owen (1876b) included additional specimens within the Theriodontia from localities other than in South Africa, namely Brithopus, Syodon (Cliorhizodon), and Deuterosaurus all from Eastern Europe, Rhopalodon from Europe, and Bathygnathus from North America. Romer (1966), however, included all these forms in the Dinocephalia except for Rhopalodon and Bathygnathus which were respectively referred to the Venyukoviamorpha and the sphenacodont pelycosaurs.

Owen (1879) added the dinocephalian Titanosuchus to the Theriodontia notwithstanding the fact that the fragmentary specimen evinced no narial characters.

In 1881 Owen extended his definition of the Theriodontia once more by incorporating in the diagnosis the additional feature of "dentition monophyodont", including at the same time another gorgonopsian, namely Aelurosaurus, in the group.

Von Zittel (1890) placed the Theriodontia as a suborder of the Theromorpha (Cope, 1878). He regarded the Theriodontia as the senior synonym of the Pelycosauria of Cope and listed it as comprising the families Cynodontia (Clepsidropidae),

Pariotichidae, Diadectidae (Cotylosauridae) and Endothiodontidae. The family Cynodontia consisted of the Sections Binarialia, Mononarialia and Tectinarialia. The first contained the North American pelycosaurids, and three South African gorgonopsids viz. Lycosaurus tigrinus (later Arctosuchus), Lycosaurus curvimola (later Arctognathus) and Tigrisuchus simus. The second included the forms from Europe, Eastern Europe and a mixture of South African gorgonopsids, cynodonts and the therocephalian Scaloposaurus constrictus whilst the third group comprised the forms Gorgonops and ?Titanosuchus.

Lydekker (1890) also regarded the suborder Theriodontia as encompassing the Pelycosauria of Cope (1878), and he combined the South African theriodonts with the North American forms, without being able to fully define the group. He recognised as families the Galesauridae, Tapinocephalidae, Diadectidae and Clepsidropidae with the family Gorgonopidae as Theriodontia incertae sedis. The Galesauridae, which included the scaloposaur Scaloposaurus and the pristerognathid Hyorhynchus, was taken as the type family of the Theriodontia, with Galesaurus planiceps the type genus of the family. Hyorhynchus platyceps (Seeley, 1889) was the first pristerognathid to be described and although Seeley (1889) recognised a similarity between it and the gorgonopsian Aelurosaurus,. he preferred rather to group it with the anomodonts because of the "pig-like" ridges on the snout and the "distinctive" palate. Lydekker (1890) synonymised

Hyorhynchus platyceps with the gorgonopsian Lycosaurus pardalis.

Von Zittel (1895) maintained the Suborder Theriodontia but recognised only two families viz. Clepsydropidae and Galesauridae. The former embraced the pelycosaurs, whilst the latter grouped the South African forms, of which the representative taxa were listed, as: Galesaurus (Nythosaurus), Cynochampsa, Cynosuchus, Lycosaurus, Tigrisuchus, Cynodraco, and Gorgonops. No mention was made of Scaloposaurus constrictus.

Seeley (1895) pointed out that the order Theriodontia created by Owen (1876a) had by that time been modified to include animals not defined by the original description. According to Seeley (1895), Owen (1876a) was the first to recognise the position of the canines and the fact that the lower canine crossed in front of the upper, as a character of ordinal importance since this feature was then unknown amongst the Reptilia. It was, however, present in a variety of mammalian orders and Seeley (1895) consequently pointed out that since it was insufficient to define any one order of mammals, he doubted whether it could be applied to the Theriodontia.

Because Seeley (1895) doubted the validity of Owen's (1876a) diagnosis of the Theriodontia he endeavoured to determine the type genus of the Theriodontia and delineate the group more precisely. He called attention to the fact that whilst Owen (1876a) regarded Lycosaurus as the type of the

Theriodontia, Zittel (1890) placed Owen's (1876a) families as sections of the family Cynodontia with Clepsydrops (ophiacodont pelycosaur, Romer 1966) as the type, whereas Lydekker (1890) placed Galesaurus as the type.

Seeley (1895) regarded the original type of Lycosaurus curvimola BMNH 47339 (Arctognathus curvimola, Sigogneau 1970) as the type of the sub-order Theriodontia which he divided into the Lycosauria, Cynodontia and the Gomphodontia. The Theriodontia was defined as follows: Occipital plate usually concave; parietal crest narrow with large temporal vacuities and zygoma into which malar bone enters; anterior nares terminal; palato-nares defined by hard palate; teeth resemble incisors, canines, and the molar teeth of mammals in form and position.

Included in the Lycosauria was Lycosaurus and the pristerognathid Pristerognathus polyodon BMNH R2581. Seeley (1895) based the genus Pristerognathus on the large number of incisors (6 upper and 3 lower) and regarded it as a variation of the condition in Lycosaurus.

From the beginning of the 20th century, however, the taxonomy of the Theriodontia was profoundly influenced, as was palaeontology in general, by the advent of Robert Broom.

Broom (1930a), in his description of Lycosuchus vanderrieti, pointed out that the Theriodontia could be divided into four groups, two of which were primitive, typified by Lycosaurus (molars simple, dentary powerful, quadrate well developed and parietal foramen large) and

Ictidosuchus (somewhat similar but with lower jaw and temporal arch very slender). The two remaining groups were highly specialised and consisted of the Cynognathus - type (molars cusped, quadrate rudimentary, parietal formen small or absent, two occipital condyles) and the similar Gomphognathus - type, allied to the former but with flattened grinding molars. Lycosuchus vanderrieti was included amongst the primitive theriodonts and despite its powerful lower jaw, Broom (1903a) regarded it to be closer to Ictidosuchus than to Lycosaurus. This astute observation was correct since Lycosaurus was a gorgonopsian. Broom (1903a) also pointed out that Lycosuchus was probably allied to the theriodont ancestor of monotremes and higher mammals and that the first mammal probably arose from a theriodont ancestor intermediate between Lycosuchus and Cynognathus, having the simple type of skull of the former but with a full set of simple molars.

Broom (1903b) proposed a new Order, namely the Therocephalia to include the primitive Theriodontia, typified by Scylacosaurus sclateri SAM 634. He pointed out that the order, as it stood, included a number of primitive forms which were not related to the typical theriodont genus Galesaurus. In these forms details of the palate could not be clearly seen and it was therefore not possible previously to establish how far they differed from typical theriodonts. In Scylacosaurus the palate was, however, visible and resembled that of the Rhynchocephalia, with the internal nares situated anteriorly as in Sphenodon and separated by long, paired vomers.

Anteriorly the vomers contact a pair of short palatal processes of the premaxillae and posteriorly the anterior extremities of the pterygoids form part of the hard palate and separate the palatines. The maxillae form no part of the palate and the pterygoid has a well-developed transverse process which contacts the ectopterygoid.

Broom (1903b) retained the name Theriodontia for what is now known as the Cynodontia and included Lycosaurus and presumably also Pristerognathus polyodon and Hyorhynchus platyceps as the most primitive members of the Therocephalia. Lycosaurus was not placed in any therocephalian family but Broom did point out that the taxon may be the type of a distinct suborder.

The Order Therocephalia was thus diagnosed as follows:

Medium sized reptiles, with temporal region supported by a single lateral arch; postfrontals usually absent (present in Scylacosaurus); postorbitals and squamosals present; supratemporals and quadratojugals absent; quadrate well developed; palate slight modification of the Rhynchocephalian type; teeth on pterygoids in Aelurosaurus and Scylacosaurus; maxillary and premaxillary teeth differentiated, as in mammals, into incisors, canines and molars; occasionally more than one pair of canines; molars simple; scapula without acromion process; probably a cleithrum; manus and pes unknown.

Family: Scylacosauridae - Distinct postfrontals present. Teeth on pterygoids, but not on palatines or prevomers. More

than one canine in each maxillary.

Genus: Scylacosaurus

Family: Aelurosauridae - Teeth on pterygoids and apparently also on palatines and prevomers. Single canine in each maxilla.

Genus: Aelurosaurus

Family: Ictidosuchidae - No distinct postfrontals. Single canine in each maxilla.

Genus: Ictidosuchus

?Family: Deuterosauridae - No palatal teeth.

Genera: Deuterosaurus

Rhopalodon

Family: Titanosuchidae - (Probably a distinct family, characters very imperfectly known)

Genus: Titanosuchus

?Family: Gorgonopsidae - Temporal region roofed, prevomers ankylosed, no palatal teeth known.

Genus: Gorgonops

Scylacosaurus sclateri SAM 634 was therefore regarded as the type genus of the Therocephalia and placed in the family Scylacosauridae. The gorgonopsian Aelurosaurus, the dinocephalian Titanosuchus and the advanced therocephalian Ictidosuchus were each referred to separate families. Although the temporal region was roofed over in Gorgonops, Broom (1903b) placed this form in the Therocephalia together with Deuterosaurus and Rhopalodon, about which little was then known. Broom (1903c) figured the palate of Scylacosaurus sclateri SAM 634 illustrating the well-developed suborbital fenestrae and pointing out that the palate was closer to that of rhynchocephalians and most other primitive reptiles than to the higher theriodonts. He regarded the Therocephalia as probably ancestral to the Theriodontia and later (1903d) pointed out additional differences between these two groups.

Broom (1903d) included two new forms viz. Ictidosaurus angusticeps and Scymnosaurus ferox in the Therocephalia together with an additional species of Lycosuchus i.e. L. mackayi. He regarded Scylacosaurus, Ictidosaurus and Scymnosaurus as typical of the new order. Aelurosaurus, Ictidosuchus and Titanosuchus were thought by him to be closely allied to Scylacosaurus whilst Lycosuchus was considered a probable therocephalian because details of the palate were then unknown. Gorgonops, in spite of its temporal region being roofed, was retained as a therocephalian. Rhopalodon and Deuterosaurus, although poorly known, were

considered as possibly aberrant therocephalians. However, disregarding the latter three genera which were of doubtful affinity, Broom (1903d) listed the differences between the Theriodontia and the Therocephalia as follows:

THEROCEPHALIA	THERIODONTIA
1. Canines 1,2, or 3; molars simple.	1. Canines single (rarely 2?) molars usually cuspid.
2. Palate a modification of the rhynchocephalian type; often bearing teeth.	2. A secondary palate formed as in mammals.
3. Quadrate well developed	3. Quadrate rudimentary.
4. Occiput with single condyle?	4. Occiput with two condyles.
5. Pineal foramen large.	5. Pineal foramen small or absent.
6. Angular and surangular large, forming large part of lower jaw.	6. Angular and surangular small- lower jaw formed almost entirely by dentary.
7. Scapula without distinct acromion.	7. Scapula with an

	acromion.
8. Precoracoid foramen entirely in precoracoid bone (Ictidosuchus).	8. Precoracoid foramen between scapula and precoracoid (Cynognathus).

Broom (1903d) was unable to place the fragmentary remains of the cynodonts Cynosuchus (Cynosaurus, Hopson & Kitching, 1972) and Cynochampsa (Diademodon, Grine, 1982) taxonomically, but regarded them together with the gorgonopsian Tigrisuchus (gorgonopsian, Haughton & Brink 1955, Theriodontia incertae sedis Sigogneau, 1970) as probable therocephalians. Lycosaurus (gorgonopsian, Haughton & Brink 1955, Theriodontia incertae sedis, Sigogneau, 1970) and Cynodraco (gorgonopsian Haughton and Brink 1955, Theriodontia incertae sedis Sigogneau, 1970) were provisionally thought by Broom (1903d) to probably belong to his higher category, Theriodontia.

Broom (1904a) regarded the genus Pristerognathus as belonging to the Therocephalia and consequently his classification (Broom, 1907b) contained the genus amongst other known therocephalians together with a number of non-therocephalian genera.

Order Therocephalia

Galechirus

Alopecodon

Pristerognathus

Lycosuchus

Glanosuchus

Hyaenasuchus

Trochosaurus

Pardosuchus

Cynodraco

Aelurosaurus

Ictidosaurus

Scylacosaurus

Scymnosaurus

Gorgonops

Cynochampsa

Cynosuchus

Scaloposaurus

Ictidosuchus

Arnognathus

Broom (1907a) considered Galechirus scholtzi, (dromasaur, Brinkman 1981) despite its lack of a coronoid process and canines, as a very primitive therocephalian-like reptile of a type from which the Anomodontia also probably were descended. Trochosaurus (see Broom 1908a, p. 366).

Broom (1908b), however, in an effort to establish interrelationships within the Therocephalia listed the known taxa as follows.

Cynochampsa laniaria

Lycosaurus pardalis

Lycosaurus tigrinus

Lycosaurus curvimola

Tigrisuchus simus

Cynodraco serridens

Cynodraco major

Cynosuchus suppostus

Scaloposaurus constrictus

Gorgonops torvus

Aelurosaurus felinus

Theriodesmus phylarcus

Hyorhynchus platyceps

Pristerognathus polyodon

Ictidosuchus primaevus

Lycosuchus vanderrieti

Lycosuchus mackayi

Scylacosaurus sclateri

Ictidosaurus angusticeps

Scymnosaurus ferox

Glanosuchus macrops

Pristerognathus baini

Scymnosaurus warreni

Alopecodon priscus

Alopecodon rugosus

Hyaenasuchus whaitsi

Trochosaurus acutus

Pardosuchus whaitsi

Arnognathus parvidens

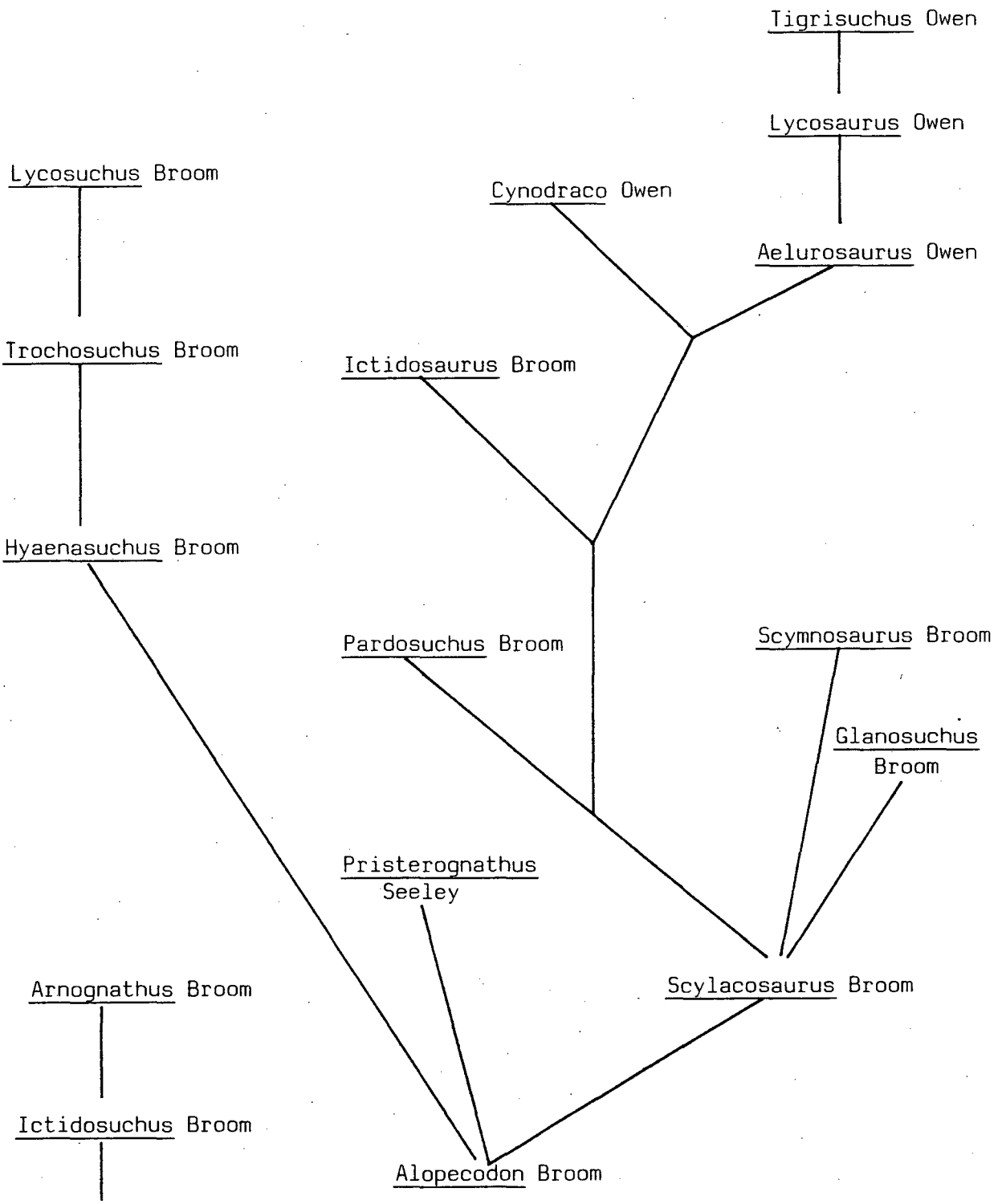
Galechirus scholtzi

Broom (1908b) now regarded Scaloposaurus constrictus, Gorgonops torvus and Galechirus scholtzi as doubtful members of the Therocephalia. He also pointed out that Hyorhynchus platyceps was too poorly preserved to be diagnosed. Trochosaurus acutus should read Trochosuchus acutus (see Broom 1908a, p. 366).

Ictidosuchus primaevus and Arnognathus parvidens were thought by him to belong to a separate therocephalian family. Lycosaurus, Tigrisuchus and Cynodraco, which occurred at a higher level, were doubtfully grouped as an advanced family whilst the remaining genera, which included Scylacosaurus sclateri, were regarded as a single family with several lines of descent. It must be pointed out here that Broom (1908b) did not name any of his proposed families. At that time the Scylacosauridae Broom (1903b) with Scylacosaurus as the type genus was the type family of the Therocephalia and Ictidosuchus was the type genus of the Ictidosuchidae Broom (1903b). The remaining families viz. Aelurosauridae, Deuterosauridae, Titanosuchidae and the Gorgonopsidae consisted of non-therocephalians.

Broom (1908b) based the interrelationships of the better known therocephalian genera on the number and type of teeth. Alopecodon, with the largest number of incisors, was regarded as ancestral to all other genera and the progressive reduction in the number of incisors and canines was thought to have given rise to successive genera along different lines of descent, which was expressed in the following manner

	Incisors	Canines	Molars
Alopecodon	VVVVVVvv	vV	VVVVVVVV
Scylacosaurus	VVVVVv	vV	VVVVVVV
Pardosuchus	VVVVVv	vV	VVVVV
Glanosuchus	VVVVVv	V	VVVVV
Ictidosaurus	VVVVv	vV	VVVVVVVV
Scymnosaurus	VVVVV	V	VVV
Pristerognathus	VVVVVV	V	VVVVVV
Hyaenasuchus	VVVVVV	VV	VVVV
Trochosuchus	VVVVV	VV	VVVV
Lycosuchus	VVVVV	VV	V



Broom (1909a) attempted to determine the stratigraphic horizons of the Karoo vertebrates and once more listed all the taxa comprising the Therocephalia. Contrary to his previous classification (Broom 1908b), Cynodraco major (Owen 1876c), Theriodesmus phylarchus (Seeley 1888) and Galechirus scholtzi (Broom 1907a) were excluded from the Therocephalia. Trochosaurus acutus, again listed in error, should read Trochosuchus acutus (see Broom 1908a, p. 366).

Broom (1910) pointed out that since he had divided Owen's Theriodontia and proposed the name Therocephalia for the Permian forms, Owen's (1861) name Cynodontia should be retained for the Triassic forms and the name Theriodontia should be dropped.

Zittel (1911) recognised the Therocephalia as primitive theriodonts, as opposed to the Cynodontia which represented the advanced theriodonts. The Scylacosauridae, Aelurosauridae, Galesauridae and Gomphognathidae were listed as representative families of the Theriodontia and the following genera were regarded by him as belonging to the Therocephalia:

Cynodraco

Cynochampsa

Tigrisuchus

Cynosuchus

Aelurosaurus

Pristerognathus

Ictidosuchus

Lycosuchus

Scylacosaurus

Ictidosaurus

Scymnosaurus

Alopecodon

Hyaenosuchus

Pardosuchus

3 Trochosuchus

Arnognathus

Lycosaurus, Inostranzewia and Bauria were considered by Zittel (1911) to be the transitional forms leading to the Cynodontia. Hyaenosuchus is an error and should read Hyaenasuchus.

Broom (1913a) again revised the classification of all the known Karoo reptiles. Contrary to his earlier contribution (Broom 1912, p. 861) where he regarded the Therocephalia as a suborder, he now placed the Therocephalia as an Order of Permian taxa listed as follows:

Order THEROCEPHALIA,

Archaeosuchus cairncrossi,

Titanosuchus ferox,

Titanosuchus cloetei,

Scapanodon duplessisi,

Scymnognathus whaitsi,

Gorgonops torvus,

Alopecodon priscus,

Alopecodon rugosus,

Lycosaurus pardalis,

Ictidosuchus angusticeps,

Eriphostoma microdon,

Lycosuchus vanderrieti,

Lycosuchus mackayi,

Pardosuchus whaitsi,

Scymnosaurus ferox,

Scymnosaurus warreni,

Glanosuchus macrops,

Trochosaurus acutus,

Hyaenasuchus whaitsi,

Scylacosaurus sclateri,

Pristerognathus polyodon

Pristerognathus baini,

Pristerognathus platyrhinus,

Lycorhinus parvidens,

Ictidognathus parvidens,

Ictidognathus hemburyi,

Scalopsaurus constrictus,

Aloposaurus gracilis,

Aelurosaurus felinis

Aelurosaurus angusticeps,

Aelurosaurus whaitsi,

Aelurosaurus striatidens,

Cynodraco serridens,

Cynosuchus suppostus,

Tigrisuchus simus,

Cynochampsa laniaria,

Arctosuchus tigrinus,

Arctognathus curvimola,

Ictidosuchus primaevus,

Arnognathus parvidens,

The taxa comprising the Therocephalia were largely identical to those included in his previous classification (Broom 1909a). In contrast, however, Archaeosuchus cairncrossi, Titanosuchus ferox, Titanosuchus cloetei and Scapanodon duplessisi, placed in the Dinocephalia by Broom (1909a), were referred to the Therocephalia by Broom (1913a). Originally Broom (1905a) regarded Archaeosuchus as a therocephalian but later (1909a) referred it to the Dinocephalia. Boonstra (1953d) transferred the specimen to Titanosuchus and questioned its specific validity (see Van den Heever and Grine, 1981 p. 85). Finally, Boonstra (1969) pointed out that the specimen was so poor that it must be regarded as a nomen dubium. Additional gorgonopsians listed by Broom (1913a) as therocephalians were Scymnognathus whaitsi, Aloposaurus gracilis, Eriphostoma microdon and three additional species of Aelurosaurus viz. A. angusticeps, A. whaitsi and A. striatidens. The two species of the gorgonopsian Lycosaurus were referred to Arctosuchus.

New therocephalians included Arnognathus parvidens, Pristerognathus (later Cynariognathus) platyrhinus, Ictidognathus (later Ictidostoma) hemburyi and Ictidognathus

parvidens.

Ictidosuchus angusticeps, Trochosaurus acutus and Lycorhinus parvidens are errors and should respectively read; Ictidosaurus angusticeps, Trochosuchus acutus and Alopecorhinus parvidens.

Broom (1913a) did however point out that Gorgonops, Titanosuchus and other allied taxa were only provisionally referred to the Therocephalia and later (Broom 1913b) re-established Seeley's Gorgonopsia as a suborder for the placement of Gorgonops and related taxa. The differences between the two groups were listed as follows:

Gorgonopsia	Therocephalia
1. Parietal region broad.	1. Parietal region narrow
2. Preparietal present	2. Preparietal absent
3. Postfrontal large	3. Postfrontal small or absent
4. Postorbital large, forming upper temporal margin and meeting squamosal above.	4. Postorbital small, not extending far back and not meeting squamosal above.
5. Single median true vomer	5. A pair of prevomers
6. Transplatine closely united to pterygoid.	6. Transpalatine separated from pterygoid by large foramen

7. Mandibles united by powerful articulated symphysis.	7. Jaws loosely
8. Angular with deep groove perforated	8. Angular

These differences, most of which are still valid at present, served effectively to remove the gorgonopsians from the Therocephalia. Unfortunately the pristerognathid Ictidosaurus was also placed in the Gorgonopsia by Broom (1913b).

Contrary to Broom (1910), Watson (1914b) provisionally retained the name Theriodontia for the Order comprising the suborders Therocephalia, Gorgonopsia, Bauridae (sic) and the Cynodontia. As well-known therocephalian specimens, he cited Scylacosaurus and the gorgonopsian Lycosaurus.

Broom (1914) pointed out that the Therocephalia was founded on the types of Scylacosaurus and Lycosuchus and that in the interests of clarity the group should be confined to these and similar taxa. In addition to the existing therocephalian families Ictidosuchidae and Scylacosauridae (Broom 1903b), Scaloposaurus and Ictidognathus were referred to the new family Scaloposauridae by Broom (1914).

Watson (1917) grouped the North American pelycosaurs and the South African therapsids in the Anomodontia and defined the Order Theriodontia as Anomodonts with carnivorous specialization, reduced quadrate and quadratojugal and a

glenoid cavity on the scapula and coracoid.

He subdivided the Theriodontia into the suborders Gorgonopsia, Cynodontia, Therocephalia and the Bauriamorpha. The Therocephalia was diagnosed as follows:

Theriodonts with a narrow intertemporal bar formed mainly by the parietals. No secondary palate. Large suborbital vacuities. Representative taxa noted were Scylacosaurus, the gorgonopsian Lycosaurus, Alopecodon, Hyaenosuchus and Pardosuchus. Hyaenosuchus is an error and should read Hyaenasuchus.

Haughton (1915) regarded the dinocephalian Titanosuchus dubius as a therocephalian. Boonstra (1969b), however, pointed out that it was identifiable only to the dinocephalian family Titanosuchidae.

Haughton (1918) described Whaitsia platyceps, establishing the family Whaitsiidae. He also recognised the family Bauriidae, a term already used by Watson (1914b) as a suborder of the Theriodontia.

Haughton (1920) maintained the classificaiton of Watson (1917) and expounded the view that the Gorgonopsia gave rise to the Cynodontia and the Therocephalia to the Bauriamorpha. He (p. 24) incorrectly regarded Whaitsia as a gorgonopsian and considered it to illustrate the change within the gorgonopsians from a broad parietal region to the narrow parietal crest of cynodonts.

New taxa included as Therocephalia were Alopecognathus, the gorgonopsian Scymnorhinus (later Broomisaurus),

Scylacorhinus, Simorhinella, Cerdodon and the gorgonopsian Lycosaurus, all from the Tapinocephalus - Zone. From the Endothiodon - Zone the gorgonopsian Scylacoides was referred to the Therocephalia.

Watson (1921) maintained his earlier (1917) division of the Theriodontia admitting that it included a variety of forms. He considered the gorgonopsians as the central theriodont group and contrary to Broom (1914 p. 31) regarded them to have given rise to the Cynodontia. Lycosaurus was figured and discussed by him as a gorgonopsian (p. 58), but also mentioned as a therocephalian with other well-known taxa like Scylacosaurus, Scymnosaurus and Scaloposaurus. In the latter case Lycosaurus is probably an error for Lycosuchus. Hyaenosuchus at p. 97 is an error and should read Hyaenasuchus.

Broili (1923) placed the Therocephalia as a Suborder of the Anomodontia. The Bauriamorpha and the Cynodontia were united in a different anomodont suborder, the Theriodontia. He regarded the Therocephalia as primitive Theriodontia and diagnosed them as follows: Skull always with large upper temporal fenestra; teeth heterodont, cone shaped, and divided into incisors, canines and molars; parietal foramen large; quadratojugal much reduced and fused with quadrate; condyle simple but partially formed by exoccipitals; jaw with large coronoid process; pelvis with medial aperture, no acromion process on scapula; vertebrae amphicoelous; Permian.

Taxa recognised by him were:

Cynodraco

Cynochampsa

Tigrisuchus

?Cynosuchus

Aloposaurus

Pristerognathus

Ictidosuchus

Lycosuchus

Scylacosaurus

Scaloposaurus

Alopecorhinus

Ictidognathus

Scymnosaurus

Alopecodon

Hyaenosuchus

Pardosuchus

Trochosuchus

Alopecognathus

Eriphostoma

Ictidosaurus

Scylacoides

Scylocorhinus

Trochosaurus

Arnognathus

Hyaenosuchus and Scylocorhinus are errors and should respectively read Hyaenasuchus and Scylacorhinus.

Nopcsa (1923, p. 122) divided the suborder Therocephalia

into the Scylacosauridae, Lycosuchidae and Whaitsiidae, thereby establishing the family Lycosuchidae. The Scaloposauridae were grouped with the suborder Gorgonopsida and the Bauriamorphidae were placed in the suborder Gomphognathia.

Haughton (1924), without listing diagnostic features, placed 5 families within the Therocephalia viz. Alopecopsidae, Ictidosuchidae, Pristerognathidae, Scaloposauridae and the Whaitsiidae.

Alopecopsidae

Alopecopsis atavus

Whaitsiidae

Whaitsia platyceps

Ictidosuchidae

Arnognathus parvidens

Cerdodon tenuidens

Ictidosuchus longiceps

Ictidosuchus primaevus

Scaloposauridae

Akidnognathus parvus

Icticephalus polycynodon

Ictidognathus hemburyi

Ictidognathus parvidens

Scaloposaurus constrictus

Simorhinella baini

Pristerognathidae

Alopecodon priscus

Alopecodon rugosus

Alopecognathus angusticeps

Alopecognathus minor

Alopecorhinus parvidens

Broomisaurus planiceps

Glanosuchus macrops

Hyaenasuchus whaitsi

Ictidosaurus angusticeps

Lycosuchus mackayi

Lycosuchus vanderrieti

Moschorhinus kitchingi

Pardosuchus whaitsi

Pristerognathus baini

Pristerognathus polyodon

Pristerognathus platyrhinus

Scylacoides ferox

Scylacorhinus falkenbachi

Scylacosaurus sclateri

Scymnosaurus ferox

Scymnosaurus warreni

Scymnosaurus watsoni

Trochosaurus intermedius

Trochosuchus acutus

Trochosuchus major

Scylacosaurus sclateri, the type genus of the Scylacosauridae (Broom, 1903b), was placed by Haughton (1924) in the Pristerognathidae, a family he erected to contain the

majority of the taxa defined as Therocephalia by previous authors viz. Broom (1913a) and Watson (1917).

Williston (1925) however, regarded the Theriodontia as a Suborder divided into 4 tribes i.e. Gorgonopsia, Bauriasauria, Therocephalia and Cynodontia. The Gorgonopsia contained the pristerognathid Scymnosaurus and the Therocephalia was grouped into 6 families. Williston (1925) retained the Whaitsiidae, Ictidosuchidae, Scaloposauridae and Alopecopsidae but a novel aspect of his classification was to group Lycosuchus, Trochosuchus and Hyaenasuchus as the family Lycosuchidae. All these specimens possessed two large canines in each maxilla and Broom (1908b) had previously pointed out that he regarded them as a separate unit.

Williston (1925), in contrast to Haughton (1924), however, placed the remaining therocephalian taxa, not in the Pristerognathidae, but in the Scylacosauridae. In this he was completely justified since the Scylacosauridae, with Scylacosaurus sclateri as the genotype, was the first therocephalian family to be erected.

Scylacosauridae

- Alopecodon
- Pardosuchus
- Glanosuchus
- Scylacosaurus
- Pristerognathus
- Ictidosaurus
- Alopecognathus

Scylacorhinus

Lycosaurus, Eriphostoma, Lycorhinus (error for Alopecorhinus), Broomisaurus (Scymnorhinus), Alopecorhinus and Scylacoides were listed as of doubtful affinity.

Nopcsa (1928) divided the Order Theriodontia into the suborders Palaeohatteroidea, Therocephaloidea, Gorgonopsoidea and Gomphognathoidea. The Suborder Therocephaloidea was diagnosed as follows: quadrate reduced; conical teeth with marked canines; parietals narrow; frontals bordering orbits; no ventral ribs; foramen obturatorium large; tail generally unknown (short?).

The Therocephaloidea was composed of 3 families:

Scylacosauridae:

Canines small; molars not reduced; suborbital vacuities on palate. Alopecodon, Alopecognathus, Anna, Cynidiognathus, Ictidoparia, Ictidosuchus, Scylacoides, Scylacorhinus, Scylacosaurus.

Lycosuchidae:

Canines large; molars reduced; suborbital vacuities present. Aelurosaurus, Alopecopsis, Glanosuchus, Moschorhinus, Trochosaurus.

Whaitsidae (sic):

Canines large; molars reduced; no suborbital vacuities. Notosollasia, Whaitsia.

None of the families included Pristerognathus. The Scaloposauridae was placed in the Suborder Gorgonopsoidea with the Gorgonopsidae and divided into 2 subfamilies, the Scaloposaurinae with Scaloposaurus and the Akidognathinae (error for Akidnognathinae) with Aelurosuchus, Akidnognathus, Icticephalus, Ictidodon, Ictidognathus, and Rhophalodon. Rhophalodon is an error and should read Rhopalodon.

The Bauriidae was classified with the cynodont families in the Suborder Gomphognathoidea.

In a rather unusual classification, Zittel (1932) placed the Therocephalia, Gorgonopsia, Bauriamorpha and Cynodontia as tribes of the Suborder Theriodontia. The Therocephalia was diagnosed as: Narrow intertemporal region of skull formed mainly by parietals; pineal foramen large; no preparietal bone; occipital condyle single; no secondary palate; pair of large suborbital vacuities in hinder part of palate; symphysis of mandible slender and loose; scapula without acromion; cleithrum rudimentary; phalangeal formula 2,3,3,3,3.

A single family, the Scaloposauridae, represented the Therocephalia and was diagnosed as: Skull shaped nearly like that of a dog; more than three pairs of incisors in upper jaw; uniform series of small simple teeth behind the canines; Permian.

The genera included in the Therocephalia were identical to that of Haughton (1924) except that Whaitsia platyceps and Ictidosaurus angusticeps were omitted. Specimens described subsequent to the classification of Haughton (1924) and which

were included as Therocephalia by Zittel (1932) were Choerosaurus dejageri and Alopecideops gracilis. Theriodesmus, although not recognised by Haughton (1924) as a therocephalian, was included by Zittel (1932), albeit doubtfully.

Broom (1932) did not propose any formal classification but chose rather to divide the Therocephalia into an earlier and a later group. The early therocephalians were those predominantly found in the Tapinocephalus Zone (Dinocephalian and Pristerognathus/Diictodon assemblage zones of Keyser and Smith, 1979) and consisted largely of Haughton's (1924) Pristerognathidae. The later therocephalians comprised the families Scaloposauridae, Whaitsiidae, Alopecopsidae and the Ictidosuchidae as recognised by Haughton (1924).

Contrary to the classification of Haughton (1924), Broom (1932) regarded the gorgonopsians Eriphostoma microdon, Lycosaurus pardalis, Arctosuchus tigrinus and Tigrisuchus simus as early Therocephalia. Haughton (1924) included Akidnognathus parvus in the Scaloposauridae whereas Broom (1932) regarded it as an early therocephalian together with the lost type of Ictidoparia brevirostris of Broom (1925). Hyorhynchus platyceps, which Broom (1908b) had invalidated, was included in the early Therocephalia although Broom (1932) admitted that the specimen was of historic interest only.

Contrary to Haughton (1924), Broom (1932) correctly excluded the gorgonopsian Broomisaurus planiceps and the two moschorhinids Moschorhinus kitchingi and Moschorhinus

(Scymnosaurus) warreni from the Pristerognathidae. He also synonymized his (1915a) taxon Trochosuchus major with Haughton's (1915) taxon Trochosaurus intermedius as Trochosaurus major. Trochosuchus acutus was, however, retained as a separate taxon. Alopecognathus minor had already been referred to Pristerognathus minor by Broom (1925) and Pristerognathus platyrhinus was referred to Cynariognathus platyrhinus by Broom (1931).

New pristerognathid taxa included by Broom (1932) were Pristerognathus vanderbyli (Broom, 1925), Alopecodon minor (Broom, 1925) and Alopecideops gracilis (Broom, 1932). The genera Ictidosaurus, Scylacosaurus, Scylacorhinus and Akidnognathus were placed in a new family, the Ictidosauridae, notwithstanding the fact that Scylacosaurus was originally regarded by him (Broom 1903b) as the type genus of the first-named therocephalian family, the Scylacosauridae. The Ictidosauridae was never recognised by other authors since it included 3 pristerognathids and the advanced therocephalian Akidnognathus. Broom (1932) established a second family, the Alopecodontidae, to include the genera Alopecodon, Pardosuchus and Alopecideops, stating that these taxa possessed three canines, two small and one large, in each maxilla.

In a 1934 revision Boonstra recognised 7 families within the suborder Therocephalia viz. Alopecopsidae, Ictidosuchidae, Pristerognathidae, Scaloposauridae, Whaitsiidae, Euchambersiidae and Lycideopsidae. The first five families were those also recognised by Haughton (1924) and the

remaining two were established for Euchambersia and Lycideops respectively.

Although Boonstra (1934) followed Haughton's (1924) classification he did point out that he was favourably disposed towards the subdivision of the Pristerognathidae as had been proposed by Williston (1925). Boonstra (1934) did not, however, recognise the family Lycosuchidae at that time but, most important of all, failed to recognise the taxonomic seniority of the Scylacosauridae over the Pristerognathidae. In addition Boonstra (1934) included Alopecodon and Scylacosaurus in the Pristerognathidae, thereby rejecting the families Alopecodontidae and Ictidosauridae of Broom (1932). Hyorhynchus and Theriodesmus were also included in the Pristerognathidae.

Boonstra (1935a) synonymized Scylacorhinus falkenbachi with Scylacosaurus sclateri, thereby including another taxon of Broom's (1932) family Ictidosauridae in the Pristerognathidae, and pointed out that he regarded the Pristerognathidae as a composite family.

This view was maintained by Boonstra (1938) who regarded the Pristognathidae as ancestral to the 6 remaining therocephalian families as well as to the advanced form Bauria. A separate line of development was thought to have led from the Pristerognathidae to the Cynodontia.

According to Broom (1936c) the Therocephalia of the Tapinocephalus Zone (Dinocephalian and Pristerognathus/Diictodon assemblage Zones of Keyser and

Smith, 1979) could be placed into either one of two possible families; one with two large functional upper canines and the other with only one functional upper canine in each maxilla. The second family also incorporated those taxa with one or two precanines.

Broom clearly had the Lycosuchidae in mind for the former family whereas the latter family would then have consisted of those taxa referred to the Scylacosauridae by Williston (1925), or the taxa remaining in Haughton's (1924) Pristerognathidae, since the two groups were similar. Broom (1932), however, had already referred the type genus of the Scylacosauridae, Scylacosaurus sclateri, to a different composite family, the Ictidosauridae but as he did not propose names for the families, his (1936c) division is meaningless.

Kuhn (1937a) followed Zittel (1932) but also included the classification of Nopsca (1928) by way of comparison.

Kuhn (1937b), on the other hand, divided the Suborder Theriodontia into 6 tribes viz. Therocephalia, Bauriamorpha, Burnetiamorpha, Gorgonopsia, Cynodontia and Ictidosauria. The Therocephalia were characterised as follows: Narrow intertemporal region consisting practically of only the parietals; sagittal crest narrow; parietal foramen large; preparietal and postfrontal absent; palate primitive; condyle single; despite mammalian digital formula of 2,3,3,3,3, the presence of suborbital fenestrae in palate illustrate distinctive character of the Therocephalia in contrast to Gorgonopsia and Cynodontia.

Kuhn (1937b) followed Boonstra (1934) in recognising 7 families within the Therocephalia viz. Alopecopsidae, Ictidosuchidae, Pristerognathidae, Scaloposauridae, Whaitsiidae, Euchambersiidae and Lycideopsidae. He regarded the Bauriamorpha as an offshoot of the Scaloposauridae, and pointed out that Watson did not regard the Scalopsauridae as typical Therocephalia because they possess a secondary palate. The Euchamberiidae was diagnosed as possessing an incomplete postorbital bar, a preorbital depression and no molars.

Von Huene (1938) also recognised the same 7 families as did Boonstra (1934) and listed the following taxa under the Pristerognathidae:

Alopecodon

Alopecorhinus

Arctosaurus

Cynariognathus

Glanosuchus

Hyaenosuchus

Hyorhynchus

Ictidoparia

Lycedops

Lycosaurus

Lycosuchus

Pristerognathus

Scymnosaurus

Scylacosaurus

Trochorhinus

Trochosaurus

Trochosuchus

Scylacoides

Alopecideops and Pardosuchus were included in the Alopecopsidae. The omission of Alopecognathus is probably an error. Arctosaurus is an error and should probably read Arctosuchus (gorgonopsian, Haughton & Brink, 1955; Theriodontia incertae sedis, Sigogneau, 1970). Hyaenosuchus is an error and should read Hyaenasuchus.

Von Huene (1938) regarded the Alopecopsidae and Ictidosuchidae as closely related to the more primitive Pristerognathidae but supported the view that the closest relationship existed between the Pristerognathidae and the small, progressive Scaloposauridae. He incongruously considered the Scaloposauridae to be both the most primitive as well as the most progressive therocephalian family and to have directly given rise to the Bauriamorpha, from which group the mammals developed via the Ictidosauria.

Camp and Vanderhoof (1940) recognised 6 families within the Therocephalia viz. Euchambersiidae, Scaloposauridae, Akidnognathidae, Scylacosauridae, Lycosuchidae and Whaitsiidae. With the exception of the Euchambersiidae, this classification was most similar to that of Nopcsa (1928) except that the Scaloposauridae which he placed in the Suborder Gorgonopsoidea was correctly referred to the Therocephalia together with the Akidnognathidae which he regarded as a subfamily of the Scaloposauridae.

In 1940 Von Huene published a classification similar to that of 1938, including Alopecognathus angusticeps and A. megalops as pristerognathids together with the gorgonopsian Arctosuchus, listed in 1938 as Arctosaurus. Trochorhinus major is however an error for Trochosaurus major.

Camp, Taylor and Welles (1942) listed the same families as comprising the Infraorder Therocephalia but in addition also recognised the Alopecopidae, Ictidosuchidae, Lycideopidae and Pristerognathidae.

Romer (1945) regarded the Therocephalia as an Infraorder of the Suborder Theriodontia. He did not recognise the Scylacosauridae of Broom (1903b), the Alopecodontidae and Ictidosauridae of Broom (1932), nor the Lycideopsidae and Euchambersiidae of Boonstra (1934), or the Lycosuchidae of Nopcsa (1923), but preferred rather to maintain 4 of the families of Haughton (1924) viz. Pristerognathidae, Alopecopsidae, Whaitsiidae and Scaloposauridae, omitting the Ictidosuchidae and including as the fifth family the Bauriidae for Bauria and its allies. The ictidosuchid taxa of Haughton (1924) were referred to the Scaloposauridae as was the pristerognathid Ictidosaurus. The lycosuchid taxa of Williston (1925) were retained in the Pristerognathidae together with Hyorhynchus, Theriodesmus, Scylacoides, the lost type of Ictidoparia and the gorgonopsians Arctosuchus and Lycosaurus. The pristerognathids Pardosuchus and Scylacosaurus were included with Alopecideops in the

Alopecopsidae. Euchambersia and Lycideops were respectively referred to the Whaitsiidae and the Scaloposauridae. The Pristerognathidae included the following taxa:

Alopecodon

Alopecognathus

Alopecorhinus

Glanosuchus

Hyaenosuchus

Hyorhynchus

?Ictidoparia

Lycedops

Lycosaurus

Lycosuchus

Pristerognathus

Scymnosaurus

?Theriodesmus

Trochorhinus

Trochosaurus

Trochosuchus

Cynariognathus

?Arctosuchus

Scylacoides

Hyaenosuchus is an error and should read Hyaenasuchus.

Von Huene (1948) defined the suborder Therocephalia as follows: Carnivorous; narrow parietal crest; no preparietal;

pineal foramen small or absent; different states in formation of a secondary palate; mostly with post palatinal opening; no palatal teeth; no chin; long posterior ascending extremity of dental; no cleithral.

He recognised the same 7 families as did Boonstra (1934) but contrary to Romer (1945) he placed Bauria and its allies in the suborder Bauriamorpha as did Watson (1917).

Von Huene (1948) placed the Pristerognathidae as the most primitive therocephalian family and regarded the Ictidosuchidae and the Scaloposauridae as ancestors respectively of the Cynodontia and the Bauriamorpha.

Broom (1948) proposed the division of the Therocephalia of the Tapinocephalus Zone into four groups based on the number and type of teeth.

1. 5-6 incisors, 2 large canines, few molars.
2. 6-5 incisors, 1 large canine, many small molars.
3. 6-7 incisors, 1 large canine and 1 or 2 small anterior canines, 5-9 small molars.
4. Small imperfectly known forms probably allied to the much later Scaloposaurids.

Broom (1948) did not name these groups but the first roughly coincides with the Lycosuchidae of Nopcsa (1923), the second with Pristerognathidae of Haughton (1924), omitting the Lycosuchid and Scylacosaurid taxa, and the third with the Ictidosauridae and the Alopecodontidae of Broom (1932). In using the upper teeth as a diagnostic feature Broom

foreshadowed later classifications where these characters would assume primary importance.

Camp, Welles and Green (1949) listed the same 10 families comprising the Infraorder Therocephalia as did Camp, Taylor and Welles (1942). Camp, Welles and Green (1953), however, included an additional family, the Alopecodontidae in the Infraorder Therocephalia. They were the first to recognise the Alopecodontidae since it was established by Broom (1932). In addition, they also listed the following non-pristerognathid taxa as Therocephalia *incertae sedis*: *Aneugomphius*, *Cerdops*, *Galecranium*, *Ictidochampsa*, *Ictidodraco*, *Leavachia* and *Silpholestes*.

In an important paper Boonstra (1953a) proposed a division of the suborder Therocephalia into two superfamilies, i.e., the Pristerosauria and the Scaloposauria, because the Scaloposauridae was thought to differ substantially from the other 8 therocephalian families.

The superfamily Pristerosauria was defined as: Therocephalians with a narrow parietal region and typically with sharp parietal crista; postorbital arch complete (except in *Euchambersia*); no secondary palate; specialized canine always present and usually very well developed; pineal foramen present (except in *Euchambersia*); postfrontal present in earlier forms, reduced or absent in later forms.

Families included in the Pristerosauria were:

Pristerognathidae

Lycosuchidae

Scylacosauridae

Ictidosuchidae

Whaitsiidae

Alopecopsidae

Lycideopsidae

Euchambersiidae

Boonstra (1953a) regarded the first three families as early and primitive with the Ictidosuchidae as a connecting link between the Pristerognathidae and the Cynodontia. The last four families were regarded as specialised, later in time, and phylogenetically sterile.

The superfamily Scaloposauria was defined as: Therocephalia with a widened parietal region and no parietal crista; postorbital arch complete in early, incomplete in later forms; incipient mammal-like secondary palate in some later forms; specialised canine sometimes absent and if present not powerfully developed; pineal foramen small and sometimes absent; postfrontal always absent.

The Scaloposauria contained the single family Scaloposauridae which Boonstra (1953a) regarded as directly ancestral to the Bauriamorpha.

Boonstra's (1953a) classification correctly gave recognition to the Scylacosauridae and differed quite markedly from that of Romer (1945) in including the Lycosuchidae, Scylacosauridae, Ictidosuchidae, Lycideopsidae and Euchambersiidae.

Boonstra (1954a) was the first to give an extensive diagnosis of the Pristerognathidae, noting that within the Tapinocephalus Zone (Dinocephalian and Pristerognathus/Diictodon Assemblage Zones of Keyser and Smith, 1979) the Pristerognathidae occurred with the Lycosuchidae, Scylacosauridae and the Scaloposauridae.

His diagnosis read as follows: Fairly small to large early carnivorous therocephalians from the Tapinocephalus-Zone with a dental formula varying within the limits I.5-6/3, C.1/1, Pc.2-9/2-9; incisors and canines usually well developed and postcanines, with few exceptions, relatively feebly developed; skull long, fairly high and narrow; snout long, fairly narrow; sagittal crest high and sharp; temporal fossa moderately long and broad; low to fairly low over postorbital arches; lower jaw strong; dentigerous ramus of dentary not curved and relatively long; post-dentary part of mandible strong; coronoid process strong; prefrontal and postorbital well developed; postfrontal well to fairly well developed; jugal arch moderate to strong; frontal with moderate entry into orbital border or excluded from it; septomaxilla with well-developed facial surface; pineal foramen medium to fairly large; parietal narrow with sharp crest; paroccipital strong; occiput deeply concave, fairly high and broad; epipterygoid narrow; anterior palatal openings medium to long; suborbital vacuities large; palate flat, with only anterior ramus of pterygoid bearing teeth; basisphenoidal tubera of medium size; parasphenoidal keel deep; suspensorium posteriorly situated

high up and only moderately laterally displaced.

Boonstra pointed out quite correctly that two groups which may eventually constitute subfamilies could be recognised within the Pristerognathidae

a. Taxa with 6 incisors and the length ofthe skull double or more that of the breadth.

b. Taxa with 5 incisors or with an inconstant 6th where the skull length is less than double the breadth.

Boonstra (1954a) included the following South African Museum specimens as Pristerognathidae:

Scymnosaurus ferox

Scymnosaurus major

Glanosuchus macrops

Ptomalestes avidus

Pristerosaurus microdon

Therioides cyniscus

Pristerognathus polyodon

Pristerognathus baini

Alopecognathus angusticeps

Alopecognathus angustioriceps

Cynariognathus paucioridens

Pristerognathoides minor

Pristerognathoides roggeveldensis

Pristerognathoides vanwyki

Pristerognathoides parvus

Maraisaurus parvus

Since only specimens held by the South African Museum were discussed by Boonstra (1954a), a number of taxa housed in other institutions were not mentioned.

A complete list of taxa was, however, given by Haughton and Brink (1955) who divided the Therocephalia into 10 families which were predominantly diagnosed by the number and the nature of the canines.

Pristerognathidae

Generalised and primitive Therocephalia with incisors, canines and molars. Narrow temporal region with sharp crest, large temporal fossae and complete postorbital bar. One canine in each maxilla. Dental formula (fide Boonstra, 1954a) I.5-6/3, C.1/1, Pc.2-9/2-9.

Lycosuchidae

Medium sized Therocephalia with two large functional canines in each maxilla.

Lycideopsidae

Extremely long dorsoventrally depressed skull, with an extremely long molar series (10 teeth) consisting of ill-developed teeth which may be absent in old age (Boonstra, 1934). Two canines in each maxilla.

Akidnognathidae

Therocephalia with incisors, canines and molars. The

maxilla carries one small canine in front of the large functional canine.

Alopecodontidae

Therocephalia with two small canines in front of the large functional canine in the maxilla.

Ictidosuchidae

Inferior temporal and postorbital bars slender, but complete. Large suborbital vacuities. Long and large temporal fossae. Large pineal foramen. Combines characters of the Pristerognathidae with some of those of the Scaloposauridae

Scaloposauridae

Skull small. Snout usually long. Intertemporal bar fairly broad. Postorbital bar either complete or incomplete but always feeble. Secondary palate in process of development. Teeth numerous and pointed with one or two small canines in front of the main canine. Pineal foramen present or absent.

Euchambersiidae

Aberrant Therocephalia, without postorbital or jugal bar, and with large preorbital depression. Molars absent. Canine with ridge on its labial surface.

Whaitsiidae

Specialised Therocephalia with no postcanine teeth. Secondary palate in process of developing in some genera. Very small suborbital foramina.

Bauriidae

Advanced Therocephalia. Teeth gomphodont. Postorbital bar incomplete in some forms. No pineal foramen. Secondary palate well developed.

Excluding the non-therocephalian families which Broom (1903b) included as therocephalian, Haughton and Brink (1955) recognised all the described therocephalian families except the Scylacosauridae of Broom (1903b), the Alopecopsidae (Haughton, 1924), and the Ictidosauridae (Broom, 1932). The reason why Haughton and Brink (1955) did not recognise the Scylacosauridae was probably due to the fact that Broom (1932) himself reassigned the type genus of the Scylacosauridae to a new family, the Ictidosauridae. However, Haughton and Brink (1955) did not recognise the Ictidosauridae either and assigned the genera comprising the composite family Ictidosauridae, i.e., the pristerognathids Ictidosaurus and Scylacosaurus (Scylacorhinus) and the advanced therocephalian Akidnognathus, to the Akidnognathidae together with the pristerognathid Trochosuchus acutus and three additional advanced therocephalians, viz. Cerdops, Cerdosuchoides and Cerdosuchus.

The Alopecopsidae (Haughton, 1924) was not recognised by Haughton and Brink (1955) because the type genus was a whaitsiid. The additional genera included in the Alopecopsidae by Romer (1945) were reassigned by Haughton and Brink (1955) to 4 different families, i.e., Pristerognathidae, Akidnognathidae, Alopecodontidae and Whaitsiidae.

They point out that Boonstra (1934) used the name Alopecopsidae in error, presumably for the Alopecodontidae. This is incorrect as Boonstra (1934) only listed the therocephalian families which he recognised at that time. That he did not recognise the Alopecodontidae is illustrated by the fact that he placed the type genus of the family, Alopecodon, with the Pristerognathidae.

At that stage the advanced Therocephalia were easily recognisable in the families Lycideopsidae, Ictidosuchidae, Scaloposauridae, Euchambersiidae, Whaitsiidae and Bauriidae. The taxa comprising these families can therefore be excluded for the purpose of this investigation. Since the Akidnognathidae and the Alopecodontidae contained some pristerognathids it would be useful to list their taxa, as well as that of the Pristerognathidae and the Lycosuchidae, as all pristerognathid taxa are discussed individually at length in the descriptive section.

Pristerognathidae

Alopecognathus angusticeps

Alopecognathus megalops

Alopecognathus angustioriceps

Alopecorhinus parvidens

Cerdodon tenuidens

Cynariognathus platyrhinus

Cynariognathus gallowayi

Cynariognathus paucioridens

Cynariognathus seeleyi

Glanosuchus macrops

Hofmeyria atavus

Ictidoparia brevisrostris

Lycedops scholtzi

Maraisaurus parvus

Notaelurodon kitchingi

Pristerognathus polyodon

Pristerognathus baini

Pristerognathus peyeri

Pristerognathus vanderbyli

Pristerognathoides minor

Pristerognathoides roggeveldensis

Pristerognathoides vanwyki

Pristerognathoides parvus

Pristerosaurus microdon

Ptomalestes avidus

Scylacoides ferox

Scymnosaurus ferox

Scymnosaurus watsoni

Scymnosaurus major

Theriodes cyniscus

Walteria skinneri

Lycosuchidae

Hyaenasuchus whaitsi

Lycosuchus vanderrieti

Lycosuchus mackayi

Trochorhinus vanhoepeni

Trochosaurus major

Trochosaurus dirus

Akidnognathidae

Akidnognathus parvus

Cerdops burgheri

Cerdosuchoides brevidens

Cerdosuchus aulodon

Ictidosaurus angusticeps

Scylacosaurus sclateri

Trochosuchus acutus

Alopecodontidae

Alopecideops gracilis

Alopecodon priscus

Ictidochampsa platyceps

Ictidodon agilis

Pardosuchus whaitsi

Von Huene (1956) followed Boonstra (1934) and recognised the same 7 therocephalian families in the suborder Therocephalia viz.

Pristerognathidae
Alopecopsidae
Lycideopsidae
Whaitsiidae
Euchambersiidae
Ictidosuchidae
Scaloposauridae

The suborder Bauriamorpha contained only Bauria and its allies.

The Pristerognathidae was diagnosed as follows: Temporal opening larger than orbit; few specimens have "step" in maxilla, close to large canine; only three genera (Hyaenasuchus, Lycosuchus and Trochosaurus) have 2 canines; canine mostly not first, but second to fourth maxillary tooth; septomaxilla large as in gorgonopsians; nares terminal and separated by dorsal process of premaxilla; frontal reaches border of orbit; nasal relatively long because snout lengthened; snout often slightly pinched in middle; vomer divides choanae and posteriorly contacts pterygoids; vomer lies at same level as palatine and pterygoid; premaxilla and maxilla form deep pits anterior to choana for lower canines; pterygoids have transverse processes between which a small interpterygoid vacuity is present; immediately anterior to

interptergyoid vacuity two small tooth rows present on pterygoids as in gorgonopsians; epipterygoid with broad base and flattened pole-like dorsal portion; lower jaw with slender, slightly curved dentary which projects a long slender process into the temporal opening; scapula broad at articulation, with slender blade and thin remnant of cleithrum; 2 coracoids; clavicula strong; interclavicula narrowed behind anterior portion and broadened posteriorly; sternal plate large; pubis platelike with obturator foramen; ilium broadened anteriorly; digits of proximal carpal and tarsal rows lengthened; phalanges reduced; confined to Tapinocephalus-Zone.

Alopecodon

Alopecognathus

Alopecorhinus

Arctosuchus

Cynariognathus

Eriphostoma

Glanosuchus

Hyaenasuchus

Hyorhynchus

Ictidoparia

Lycedops

Lycosaurus

Lycosuchus

Maraisaurus

Porosteognathus

Pristerognathus

Pristerosaurus

Pristerognathoides

Ptomalestes

Scylacoides

Scylacosaurus

Scymnosaurus

Theriodesmus

Therioides

Trochosaurus

Trochosuchus

Walteria

The Alopecopsidae were diagnosed as follows: Distinguished from the closely related pristerognathids by a slender, long snout and a much lower, slender dentary; relatively small animals; few (Alopecopsis, Notaelurops) have no postcanines; postfrontal may be absent.

Alopecideops

Pardosuchus

Scylacocephalus

Scylacorhinus

Arctosuchus

Alopecopsis

Hofmeyria

Notaelurodon

Notaelurops

Proalopecopsis

Promoschorhynchus

Von Huene's (1956) composite family Alopecopsidae included the pristerognathids Alopecideops, Pardosuchus and also Scylacorhinus, since he did not recognise Boonstra's (1935) synonymy of Scylacorhinus with Scylacosaurus.

The remaining genera consisted of gorgonopsians i.e. Scylacocephalus, which he figured, whaitsiids, and advanced therocephalians. The pristerognathid Ictidosaurus was included in the Ictidosuchidae together with Alopecodon which was also included in the Pristerognathidae.

Contrary to Von Huene (1956), Romer (1956) restricted the infraorder Therocephalia to the families Pristerognathidae, Trochosuchidae, Whaitsiidae and Euchambersiidae. The remaining taxa were placed in the Bauriamorpha. The lycosuchid taxa were incorrectly separated as the Trochosuchidae, since the family name Lycosuchidae (Nopcsa, 1923) was based on Lycosuchus and therefore had precedence.

Pristerognathidae

Large primitive therocephalians; face heavy and rounded in section; temporal fossa long; sagittal crest developed; suborbital vacuities large; upper incisors up to 7 in number; 3-9 simple cheek teeth; occiput deep and triangular in outline; canine single, dentary deep with lower border essentially straight.

Pristerognathidae

- ?Akidognathus
- Alopecideops
- Alopecodon
- Alopecognathus
- Alopecorhinus
- Cynariognathus
- Glanosuchus
- ?Hyorhynchus
- Ictidoparia
- Ictidosaurus
- Lycedops
- Maraisaurus
- ?Notaelurodon
- Pardosuchus
- Pristerognathoides
- Pristerognathus
- Pristerosaurus
- Ptomalestes
- Scylacoides
- Scylacorhinus
- Scylacosaurus
- Scymnosaurus
- ?Tamboeria
- Therioides
- Walteria

Trochosuchidae

Resembles Pristerognathidae in basic features, but skull lower and snout broad and flattened; occiput wider; sagittal crest not elevated; normally 2 canines.

Hyaenasuchus

Lycosuchus

Trochorhinus

Trochosuchus

Trochosuchus appears to have included Trochosaurus also.

Watson and Romer (1956) followed Romer (1956) and divided the Infraorder Therocephalia into the same 4 families but amended the diagnoses and constituent taxa of the Pristerognathidae and Trochosuchidae.

Pristerognathidae

Large therocephalians; narrow parietal crest usually elevated; parietal foramen situated well forward; postfrontal generally fairly large; face heavy and rounded in transverse section; temporal fossa large; quadrates unexpectedly small; palate essentially flat; large suborbital vacuities; occiput commonly deep, triangular, and with dermosupraoccipital not reaching summit of back of skull; usually large number of incisors, up to 7; canine single; molars 3-9; may be small interpterygoid vacuity between transverse flanges and another where deepened median parasphenoidal ridge separates borders of pterygoid; lower

border of dentary usually straight, rounding off to anterior extremity; dentaries usually not fused.

Watson and Romer (1956) listed the same taxa for the Pristerognathidae as did Romer (1956) with only 3 exceptions. Akidnognathus was regarded as Bauriamorpha incertae sedis, Notaelurodon was regarded as Therocephalia incertae sedis, and Tamboeria was placed as Therapsida incertae sedis.

Trochosuchidae

Large therocephalians which resemble Pristerognathidae in fundamental features; skull much lower than pristerognathids; snout broad and rather flattened; sagittal crest never elevated; occiput transversely widened; may have 6 incisors; two canines each separately replaced.

Watson and Romer (1956) retained the family Trochosuchidae with the same genera as Romer (1956) and synonymized Trochosaurus, Haughton (1915) with Trochosuchus, Broom (1908a).

Camp and Allison (1961) and Lehman (1961) recognised the same 4 therocephalian families as Watson and Romer (1956), the latter largely including the same taxa in the Pristerognathidae. Contrary to Watson and Romer (1956) Lehman (1961) included Cerdodon and Notaelurodon as doubful pristerognathids, omitted Hyorhynchus and Pardosuchus, and regarded Alopecideops, Alopecodon, Alopecorhinus, Ictidoparia, Ictidosaurus, Scylacoides and Walteria (later Karoowalteria) as incompletely known and of doubtful affinity.

Lehman's diagnosis of the Pristerognathidae is identical to that of Boonstra (1954a) except that he stated that the quadrate is very small, as did Watson and Romer 1956). This is, however, not strictly true since the quadrate is still relatively large in pristerognathids, although considerably smaller than in gorgonopsians.

Lehman (1961) agreed with Watson and Romer (1956) in the definition of the lycosuchid Therocephalia, also preferring the family name Trochosuchidae, but listing Trochosaurus as presumably the senior synonym of Trochosuchus.

Apart from the Whaitsiidae and the Euchambersiidae the remainder of the therocephalian genera were included in the Bauriamorpha under 7 families.

Kuhn (1961) divided the Infraorder Therocephalia into 5 families viz. Pristerognathidae (including the Scylacosauridae of Broom, 1903b), the Trochosuchidae, the Whaitsiidae, the Euchambersiidae and the Annidae. The bauriids were placed in the Infraorder Bauriamorpha. The Pristerognathidae were diagnosed as: Large; facial region round in section; long temporal region with sagittal crest; close to all other families. The Trochosuchidae was diagnosed as: Very close to the Pristerognathidae but skull lower, snout wide and flat. In an addendum Kuhn (1961 p.79) pointed out that the name Anna was preoccupied and instead proposed the name Annatherapsidus which was placed in a new family, the Annatherapsidae to replace the Annidae.

Camp, Allison and Nichols (1964) recognised only the

Pristerognathidae, Trochosuchidae, Euchambersiidae, Annidae and Whaitsiidae but Boonstra (1964) kept the Scylacosauridae and Pristerognathidae as separated families.

Vjuschkov (1964) equated the Therocephalia with the Superfamily Scylacosauroidea which he divided into 7 families viz. Pristerognathidae, Scylacosauridae, Alopecodontidae, Annidae, Lycosuchidae, Whaitsiidae and the Euchambersiidae. The remaining therocephalian genera were placed in the Superfamily Ictidosuchoidea (Bauriamorpha).

This classification was based mainly on the number and nature of the canines. Scylacosaurus, Scylacorhinus and Ictidosaurus were placed in the Scylacosauridae, in contrast to Romer (1956) and Watson & Romer (1956) who retained these genera in the Pristerognathidae. Romer (1956) and Watson & Romer (1956) also did not recognise the Alopecodontidae and included Alopecideops, Alopecodon and Pardosuchus in the Pristerognathidae. Anna and Chthonosaurus were regarded as probable whaitsiids by Watson & Romer (1956) but placed as Therocephalia incertae sedis. Romer (1956) did not mention the latter two genera. The diagnosis of Vjuschkov (1964) thus read as follows:

Pristerognathidae:

Medium sized primitive therocephalians, with high rounded snout; enlarged incisors and one large canine; only Porosteognathus possesses two maxillary canines; frontal and prefrontal large; postfrontal always present; parietal

foramen relatively large; occiput high and triangular. Lower border of dentary straight; tooth formula I.2-7/3, C.1-2/1, Pc.3-9/3-9.

Alopecognathus

Alopecorhinus

Cynariognathus

Glanosuchus

Hyorhynchus

Ictidoparia

Lycedops

Maraisaurus

Porosteognathus

Pristerognathoides

Pristerognathus

Pristerosaurus

Ptomalestes

Scylacoides

Scymnosaurus

Therioides

Walteria

?Notaelurodon

?Tamboeria

Scylacosauridae

Small to medium-sized therocephalians very near to the Pristerognathidae but possess 2 canines of which the anterior

one is very small.

Akidnognathus

Cerdops

Cerdosuchus

Ictidosaurus

Scylacorhinus

Scylacosaurus

Cerdosuchoides

Alopecodontidae

Small to medium-sized therocephalians close to the Pristerognathidae, but with two small maxillary canines anterior to the large permanent, functional canine. Snout generally low.

Alopcideops

Alopecodon

Pardosuchus

Ictidochampsa

Urumchia

Annidae

Small to medium-sized therocephalian; 2 canines in upper jaw; anterior canine small; rudimentary palatal bulge on maxilla; teeth on pterygoid; jugal arch narrow; parietal foramen absent.

Anna

Chthonosaurus

Lycosuchidae

Medium-sized therocephalians with 5-6 incisors and 2 large functional maxillary canines; otherwise close to Pristerognathidae but skull flatter, snout broader and lower, sagittal crest higher, occiput broader.

Hyaenasuchus

Lycosuchus

Trochorhinus

Trochosuchus (Trochosaurus)

Kuhn (1965) recognised 6 families within the Infraorder Therocephalia viz. Annatherapsidae, Pristerognathidae, Akidnognathidae, Lycosuchidae, Whaitsiidae and Euchambersiidae. The Scylacosauridae (Broom, (1903b) and Alopecodontidae (Broom, 1932) were placed as junior synonyms of the Pristerognathidae. Kuhn (1965) did point out though that the Scylacosauridae was the oldest family name and therefore probably the senior synonym. He was, however, not convinced that Scylacosaurus and Pristerognathus belonged to the same family. The Annatherapsidae included Annatherapsidus petri and Chthonosaurus velocidens. The Pristerognathidae, in addition to the same taxa recognised by Watson and Romer (1956), also included Porosteognathus, Tamboeria and doubtfully, Notaelurodon. Contrary to Watson and Romer (1956), Kuhn (1965) did not recognise the Family Trochosuchidae but correctly referred the same taxa i.e.

Hyaenosuchus, Lycosuchus, Trochorhinus and Trochosuchus (Trochosaurus) to the Lycosuchidae. Hyaenosuchus is an error for Hyaenasuchus. Theriodesmus was grouped with the Therocephalia but considered unidentifiable.

Romer (1966) divided the infraorder Therocephalia into 5 families viz. Pristerognathidae, Alopecodontidae, Trochosauridae (Lycosuchidae), Whaitsiidae and the Euchambersiidae. The remaining families of advanced therocephalians were grouped under the Infraorder Bauriamorpha.

Romer (1966) retained the Alopecodontidae with the same genera as Vjuschkov (1964). However, the taxa placed in the Annidae (Annatherapsidae, Kuhn 1961, p. 79 by Vjuschkov (1964) and Kuhn (1965) were included in the Pristerognathidae by Romer (1966), and the lycosuchid genera were grouped in a new family, the Trochosauridae, which superseded the Trochosuchidae, a name established independently by Romer (1956). Van den Heever (1980) pointed out that this was probably done because Romer (1966) no longer regarded Trochosuchus as a lycosuchid, and included it in the Alopecodontidae in spite of the fact that Watson & Romer (1956) had synonymized Trochosaurus with Trochosuchus in the family Trochosuchidae together with the other lycosuchid genera.

However, Williston's (1925) and Haughton & Brink's (1955) use of the name Lycosuchidae has precedence over both the Trochosauridae and Trochosuchidae because Nopcsa had

established the Lycosuchidae in 1923. Van den Heever (1980) incorrectly attributed the establishment of the Lycosuchidae to Haughton and Brink (1955).

Pristerognathidae

- ?Akidnognathus
- Alopecognathus
- Alopecorhinus
- Anna
- Chthonosaurus
- Cynariognathus
- Glanosuchus
- ?Hyorhynchus
- Ictidoparia
- Ictidosaurus
- Karroowalteria (Walteria)
- Lycedops
- Maraisaurus
- Mirotenthes
- ?Notaelurodon
- Porosteognathus
- Pristerognathoides
- Pristerognathus
- Pristerosaurus
- Ptomalestes
- Scylacoides
- Scylacorhinus

Scylacosaurus

Scymnosaurus

?Tamboeria

Therioides

Alopecodontidae

Alopecideops

Alopecodon

Pardosuchus

Trochosuchus

?Urumchia

Trochosauridae (Lycosuchidae)

Hyaenasuchus

Lycosuchus

Trochorhinus

Trochosaurus

Appleby, Charig, Cox, Kermack and Tarlo (1967) following Olson (1962) regarded the Therocephalia as a Superfamily and contrary to Romer (1966) recognised the same 4 families as Romer (1956).

Camp, Allison, Nichols & McGinnis (1968) included 6 families within the infraorder Therocephalia viz. Annidae, Euchambersiidae, Pristerognathidae, Moschorhinidae, Trochosuchidae and Whaitsiidae. They did not recognise the Annatherapsidae established by Kuhn (1961).

Kalandadse et al.(1968) and Tatarinov (1968), in papers on the theriodonts from the USSR recognised 4 families within the Suborder Therocephalia viz. Pristerognathidae, Scylacosauridae, Annatherapsididae (sic) and the Whaitsiidae. The Suborder Scaloposauria included the Bauriamorpha and the family Ericiolacertidae. Because of the relative paucity of theriodonts from the USSR these classifications are not fully representative of the Therocephalia as a group.

Boonstra (1969b), contrary to Vjuschkov (1964) but in agreement with Romer (1966), recognised the Infraorder Therocephalia and stated that the group was represented in the Tapinocephalus Zone (Dinocephalian and Pristerognathus/Diictodon Assemblage Zones of Keyser and Smith, 1979) by 4 families viz. Pristerognathidae, Lycosuchidae, Alopecodontidae and Scaloposauridae.

Pristerognathidae

Primitive Therocephalia with 5-6 incisors; canine single; 2-9 variable postcanines; epipterygoid narrow.

The Pristerognathidae were divided into two subfamilies, the Scymnosaurinae and Pristerognathinae. This division was already indicated by Boonstra (1954a).

Scymnosaurinae

Fairly large to large pristerognathids with 5 incisors and 2-6 postcanines.

Glanosuchus macrops

Pristerosaurus microdon

Ptomalestes avidus

Scymnosaurus ferox

Scymnosaurus major

Scymnosaurus watsoni

Zinnosaurus paucidens

Pristerognathinae

Boonstra (1969b) gave no formal diagnosis of this subfamily but grouped taxa in which the upper teeth fell within the dental formula I.5-6, C.1, Pc.4-9.

Alopecognathus angusticeps

Alopecognathus angustioriceps

Alopecognathus megalops

Alopecognathus skinneri

Cynariognathus gallowayi

Cynariognathus paucioridens

Cynariognathus platyrhinus

Cynariognathus seeleyi

Lycedops scholtzi

Pristerognathoides minor

Pristerognathoides parvus

Pristerognathoides peyeri

Pristerognathoides roggeveldensis

Pristerognathoides vanderbyli

Pristerognathoides vanwyki

Therioides cyniscus

Lycosuchidae

Early fairly large Therocephalia with fairly broad flattened skulls with two functional canines in the maxilla; advanced broadened epipterygoid and low sagittal crest; otherwise very similar to pristerognathids.

Hyaenasuchus

Lycosuchus

Trochorhinus

Trochosaurus

Alopecodontidae

Fairly small early Therocephalia; 2 small canines in maxilla anterior to single large canine.

Alopecideops gracilis

Alopecodon priscus

Pardosuchus whaitsi

The Scaloposauridae did not inlcude any pristerognathids.

Camp et al.(1972) recognised 7 families within the Infraorder Therocephalia viz. Akidnognathidae, Annidae, Euchambersiidae, Pristerognathidae, Moschorhinidae, Trochosuchidae and Whaitsiidae. They did not recognise the Annatherapsidae of Kuhn (1961) and regarded Cerdops, Cerdosuchoides, Cerdosuchus and Proalopecopsis as Therocephalia incertae sedis.

Boonstra (1972) proposed a classification where the Order

Therocephalia consisted of the families Pristerognathidae, Lycosuchidae and Whaitsiidae. The rest of the therocephalians were grouped as the Order Scaloposauria, divided into the Suborder Ictidosuchia with the families Alopecodontidae, Ictidosuchidae and Scaloposauridae, and the Suborder Bauriamorpha with the families Bauriidae and Ericiolacertidae.

Pristerognathidae

Middle Permian therocephalians with well-developed dentition with single canine; no secondary palate; epipterygoid slender postfrontal small; suborbital fenestra large.

Lycosuchidae

Middle Permian therocephalians with well-developed carnivorous dentition; canines double; no secondary palate; epipterygoid widened; postfrontal small; suborbital fenestra large.

Tatarinov (1974) divided the suborder Therocephalia into two Superfamilies viz. Scylacosauroidea and Whaitsioidea. The Scylacosauroidea comprised 2 families, the Scylacosauridae and the Pristerognathidae. The former consisted of two subfamilies i.e. Alopecodontinae and Scylacosaurinae.

Scylacosauridae

Premaxillae with narrow palatal processes bordering on inside of palatal apertures; parietal region relatively wide,

not forming sagittal crest; maxilla with precanines; some specimens with 5 terminal lower incisors; dental formula I.5-7/5, C.1+1-2/1, Pc.3-10/3-8.

Alopecodontinae

Maxilla with 2 precanines; dental formula I.6-7, C.1+2, Pc.5-7.

Pardosuchus

Alopecodon

Alopecideops

Hexacynodon

Scylacosaurinae

Maxilla with 1 precanine; dental formula I.4-6/5, C.1+1/1, Pc.3-10/3-8; skull elongated with long snout; orbit small; temporal opening large.

Scylacosaurus

Ictidosaurus

Trochosuchus

Akidnognathus

?Ictidoparia

Cerdosuchus

Cerdosuchoides

Cerdops

?Urumchia

Scylacosuchus

Pristerognathidae

Skull long, high and narrow; palatal portion of premaxilla broad, not emarginated posteriorly by internal choanae; well developed sagittal crest; preorbital depression large; frontal usually forms small portion of dorsal border of orbit; occiput vertical with deeply concave sides; interpterygoid vacuity "therocephalian", small and located anterior to basisphenoid; some authors recorded small vacuity between transverse processes of pterygoids (Boonstra, 1954); ventral basisphenoid keel strongly developed; jaw articulation located slightly below level of alveolar border of maxilla (Boonstra, 1953); lower jaw with well developed coronoid process; always teeth on anterior process of pterygoid; no teeth recorded on transverse process of pterygoid (Boonstra, 1954); no precanines in maxilla; precanine diastema sometimes absent; step anterior to canine in alveolar border of maxilla usually not present; teeth slightly curved, usually with serrated posterior edge; incisors and canines strong, postcanines weak, lower jaw with 3 incisors except Notaelurodon which has 4; dental formula: I.5-6/3-4, C.1/1, Pc.2-9/2-9.

Alopecognathus

?Alopecorhinus

Cynariognathus

Glanosuchus

Hyorhynchus

Karoowalteria

Lycedops

Maraisaurus

?Notaelurodon

Porosteognathus

Pristerognathus

Pristerognathoides

Pristerosaurus

Ptomalestes

?Scylacoides

Scymnosaurus

?Tamboeria

Therioides

Zinnosaurus

The Lycosuchidae were grouped in the Superfamily Whaitsioidea with amongst others, the advanced families Whaitsiidae and Euchambersiidae.

Kitching (1977) followed the classification of Boonstra (1969b) with minor alterations. In contrast to Tatarinov (1974) he retained the Infraorder Therocephalia and divided it into 7 families viz. Pristerognathidae, Lycosuchidae, Alopecodontidae, Whaitsiidae, Moschorhinidae, Euchambersiidae and Akidnognathidae. The Pristerognathidae comprised two subfamilies, the Scymnosaurinae and the Pristerognathinae. The infraorder Scaloposauria consisted of the Scaloposauridae, Ictidosuchidae and doubtfully the Lycideopsidae, whilst the Infraorder Bauriamorpha consisted of the single family

Bauriidae. An additional therocephalian family, the Trochosauridae (Lycosuchidae) containing Hyaenasuchus whaitsi and Trochosaurus major (Kitching 1977, p. 42) appears to be an oversight since Trochosaurus major was also included in the Lycosuchidae (Kitching 1977, p. 32) and the latter family has precedence (Nopcsa 1923).

Kitching (1977) retained the Alopecodontidae in the infraorder Therocephalia in contrast to Boonstra (1972) who placed it in the Order Scaloposauria with the Ictidosuchidae and Scaloposauridae.

According to Kitching (1977, p. 31) Boonstra (1934) subdivided the Infraorder Therocephalia into Pristerognathids, Ictidosuchids, Whaitsiids and Scaloposaurids. This is incorrect as Boonstra (1934, p. 215) stated: "The Suborder Therocephalia has hitherto been subdivided into 5 families, viz. Alopecopsidae, Ictidosuchidae, Pristerognathidae, Scaloposauridae and Whaitsidae (sic); to these must now be added the Euchambersidae (sic) and the Lycideopsidae."

Within the Scymnosaurinae Kitching (1977) recognised the same taxa as Boonstra (1969b) but differed from the latter in the composition of the Pristerognathinae. Boonstra (1969b) regarded Pristerognathus polyodon as a nomen dubium whilst Kithing (1977) felt that the taxon was valid on the basis of Mendrez (1972a, 1975a). Pristerognathus baini and Ictidosaurus angusticeps were also listed by Kitching (1977) but he pointed out that Boonstra (1935a) regarded the latter as unidentifiable and had placed the former as a nomen dubium.

Boonstra (1969b p.51) referred Karroowalteria to Pristerognathoides but listed it as Alopecognathus skinneri (p. 57). Kitching (1977) also listed the specimen as Alopecognathus skinneri.

Kitching (1977) agreed with Boonstra (1969b) on the composition of the Alopecodontidae but also included Trochosuchus acutus, following Romer (1966). Boonstra (1969b) apparently regarded Trochosuchus as a synonym of Trochosaurus; Tatarinov (1974), on the other hand, placed it in the Scylacosaurinae. Tatarinov (1974) regarded the Alopecodontidae as a subfamily, the Alopecodontinae which, in addition to Hexacynodon, from the USSR, contained the same taxa as in the classification of Boonstra (1969b).

Kitching (1977) followed Tatarinov (1974) by not recognising the Scylacosauridae and he referred Scylacosaurus sclateri and Ictidosaurus angusticeps to the Pristerognathidae, Trochosuchus, Pardosuchus, Alopecodon and Alopecideops to the Alopecodontidae, Akidnognathus to the Akidnognathidae, the lost type of Ictidoparia to the Pristerognathidae, and the remaining South African taxa, i.e. Cerdops, Cerdosuchus and Cerdosuchoides, to the Moschorhinidae. In addition Alopecorhinus parvidens, Scylacoides ferox, Hofmeyria atavus and Notaelurodon kitchingi were doubtfully referred to the Pristerognathidae by Kitching (1977) whilst Cerdodon tenuidens was regarded as a nomen dubium. Boonstra (1934) placed Cerdodon in the Ictidosuchidae but Kitching (1977) followed Haughton and Brink (1955) who

regarded the taxon as a pristerognathid. Hyorhynchus platyceps was also included in the Pristerognathidae although Boonstra (1969b) pointed out that the specimen was only identifiable to family level. Lycosuchus mackayi was regarded as Theriodontia incertae sedis by Kitching (1977).

Pristerognathidae

Subfamily Scymnosaurinae

Scymnosaurus ferox

Glanosuchus macrops

Ptomalestes avidus

Scymnosaurus major

Zinnosaurus paucidens

Pristerosaurus microdon

Scymnosaurus watsoni

Subfamily Pristerognathinae

Alopecognathus angusticeps

Alopecognathus angustioriceps

Alopecognathus megalops

Alopecognathus skinneri

Alopecorhinus parvidens

Cerdodon tenuidens

Cynariognathus paucioridens

Cynariognathus platyrhinus

Cynariognathus gallowayi

Cynariognathus seeleyi

Hyorhynchus platyceps

Ictidoparia brevirostris

Ictidosaurus angusticeps

Hofmeyria atavus

Lycedops scholtzi

Notaelurodon kitchingi

Pristerognathoides minor

Pristerognathoides parvus

Pristerognathoides peyeri

Pristerognathoides roggeveldensis

Pristerognathoides vanderbyli

Pristerognathoides vanwyki

Pristerognathus baini

Pristerognathus polyodon

Scylacoides ferox

Scylacosaurus sclateri

Therioides cyniscus

Lycosuchidae

Hyaenasuchus whaitsi

Lycosuchus vanderrieti

Trochorhinus vanhoepeni

Trochosaurus major

Alopecodontidae

Alopecideops gracilis

Alopecodon priscus

Pardosuchus whaitsi

Trochosuchus acutus

Mendrez (1975a) established a new therocephalian family, the Crapartinellidae, based on the small, poorly preserved partial skull of Crapartinella croucheri. This family was not recognised by Kitching (1977) and may be based on a juvenile specimen.

Anderson and Cruickshank (1978) recognised only the family Pristerognathidae, in which the South African forms were represented by the single genus Pristerognathus. Porosteognathus, a fragmentary specimen from the USSR was also included in the Pristerognathidae by them.

Kemp (1982) recognised 8 families within the Suborder Therocephalia viz. Crapartinellidae, Pristerognathidae, Moschorhinidae, Whaitsiidae, Ictidosuchidae, Scaloposauridae, Ericiolacertidae and the Bauriidae.

Hopson and Barghusen (1986), in the first detailed cladistic overview of therapsid relationships, placed the single family Pristerognathidae as the sister group of all the other therocephalian taxa which they grouped in the families Hofmeyriidae, Euchambersiidae, Whaitsiidae, Ictidosuchidae, Ictidosuchopsidae, Regisauridae, Lycideopsidae, Ericiolacertidae and Bauriidae. The Pristerognathidae were diagnosed as: Lower incisor number reduced from 4 to 3; vomers transversely expanded beyond the primitive therocephalian condition; premaxilla with prominent vomerine process broadly overlapping ventral surface of the vomer.

Broom (1932) based the families Alopecodontidae and Ictidosauridae on the number of precanine maxillary teeth. The Alopecodontidae were diagnosed by the possession of 2 precanines and the Ictidosauridae by the possession of 1 precanine. The first authors other than Broom (1932) to recognise the Alopecodontidae were Camp, Welles and Green (1953). Subsequently the family was recognised by others such as Haughton and Brink (1955), Vjuschkov (1964), Romer (1966), Boonstra (1969b) and Kitching (1977). Tatarinov (1974) recognised it only as the Subfamily Alopecodontinae. The Ictidosauridae was never recognised by any other author.

Precanines are present within the Therocephalia amongst a number of pristerognathid as well as non-presterognathid taxa. The maximum number of precanines amongst known pristerognathids is two, as in the holotype of Alopecodon priscus. Contrary to Hopson and Barghusen (1986), two precanines are also present in their new combined family, the Euchambersiidae (= Annatherapsididae, Moschorhinidae, Akidnognathidae), as is shown by the undescribed specimen FMNH UR2462 from Wagenaarskraal, Victoria West. In addition, since the Akidnognathidae is the oldest family name in this grouping, it should have priority.

Consequently, the number of precanine teeth alone is not sufficient to diagnose family or subfamily group taxa. This feature is, however, regarded here as diagnostic at specific level, and the families Alopecodontidae and Ictidosauridae are therefore considered invalid.

Mendrez (1972a) noted that the Pristerognathidae and the Lycosuchidae probably comprised a single family because both Pristerognathus polyodon and Ptomalestes avidus possess a second canine alveolus in each maxilla. She regarded this condition as indicating the presence of two functional canines in each maxilla, a feature until then thought to be diagnostic of the Lycosuchidae only. It seemed therefore as if Mendrez (1972a) had tentatively synonymized the Pristerognathidae with Lycosuchidae and not vice versa. Later, however, (Mendrez, 1975a), she retained Pristerognathus polyodon as a pristerognathid.

Van den Heever (1980) agreed that the features which at that time separated the Pristerognathidae and the Lycosuchidae were non-diagnostic and that the two taxa comprised a single family in which two canine alveoli were present in each maxilla. In addition he showed that in these taxa the canines were not simultaneously, but alternately functional and that the basis for recognising the family Lycosuchidae was therefore invalid. Kermack (1956) had already noted alternate canine replacement in the Therocephalia but he incorrectly maintained that in the Lycosuchidae both canine alveoli bore functional canines simultaneously.

Broom (1903b) erected the Scylacosauridae as the type family of the Therocephalia. This was followed by Nopcsa (1923) who, in addition, established the family Lycosuchidae. Haughton (1924), however, chose to unite the Scylacosauridae and the Lycosuchidae as the Pristerognathidae without stating

the taxonomic basis for this action. According to the International Code of Zoological Nomenclature, Article 23 states: 'The valid name of a taxon is the oldest name applied to it', and in section d(i) it is further stated that: 'A family-group taxon formed by the union of two or more taxa of that group takes the oldest valid family-group name among those of its components, with change of termination if required'.

The reason that Haughton (1924) did not recognise the Scylacosauridae was probably the fact that he regarded Pristerognathus (Seeley, 1895) as the oldest described taxon. He did not recognise Hyorhynchus platyceps (Seeley 1889), which is so badly preserved that even Broom (1908b) acknowledged that it could not be diagnosed. However, according to Article 64 of the International Code of Zoological Nomenclature, a zoologist establishing a new family group taxon is free to choose as type genus any included nominal genus, not necessarily that bearing the oldest name.

Williston (1925) correctly included the pristerognathid taxa of Haughton (1924) in the Scylacosauridae. However, subsequent authors viz. Boonstra (1934, 1938), Romer (1945), and Von Huene (1948), all followed Haughton (1924) in recognising the Pristerognathidae at the cost of the Scylacosauridae. Broom (1932, 1948), without actually naming the family, appears to have recognised the Pristerognathidae as well as the Lycosuchidae, but referred Scylacosaurus to his new family Ictidosauridae.

Boonstra (1953a, 1954a) recognised both the Pristerognathidae and the Scylacosauridae, in contrast to Haughton and Brink (1955), Von Huene (1956), Romer (1956) and Lehman (1961), all of whom recognised only the Pristerognathidae. With the exception of Haughton and Brink (1955), who placed Scylacosaurus in the Akidnognathidae, all these authors included Scylacosaurus as a pristerognathid.

In contrast, Vjuschkov (1964) recognised both the Pristerognathidae and the Scylacosauridae, and included all the therocephalian families in the Superfamily Scylacosauroidea, a view supported by Kalandadse et al. (1968) as well as Tatarinov (1968). Romer (1966) recognised the Pristerognathidae but not the Scylacosauridae, as did Boonstra (1969b, 1972). Kuhn (1966) recognised the Infraorder Therocephalia (=Scylacosauroidea Vjuschkov 1964, Pristerosauria Boonstra 1953a) but contrary to Romer (1966) retained the familial classification of Vjuschkov (1964) with two exceptions only. The family Annidae was renamed Annatherapsidae and Akidnognathus was placed in the family Akidnognathidae, following Haughton & Brink (1955). Contrary to Kuhn (1966) Nopcsa (1928), in spite of a lapsus calami, retains original authorship of the family Akidnognathidae, and not Haughton and Brink (1955). The latter authors only effected a change in rank and a justified emendation. In addition Kuhn (1966) correctly pointed out that should the Pristerognathidae and the Scylacosauridae be united, the resulting family may not be known as the Pristerognathidae.

Tatarinov (1974) recognised the Scylacosauridae and the Pristerognathidae and divided the former into two subfamilies, the Alopecodontinae and the Scylacosaurinae. The Alopecodontinae was chiefly diagnosed by the possession of 2 maxillary precanines and the Scylacosaurinae by the possession of 1 maxillary precanine. Kitching (1977), Kemp (1982), and Hopson and Barghusen (1986) recognised only the Pristerognathidae.

As a result of this investigation, it has become clear that a new disposition of the known early Therocephalia has become necessary. Historically the Scylacosauridae is the valid type family name of the Therocephalia. Consequently, despite the fact that the name Pristerognathidae has become entrenched in the literature through time and usage, the name Scylacosauridae has precedence over the name Pristerognathidae and the latter should therefore be considered a junior synonym.

MATERIAL AND METHODS

The specimens discussed in this paper constitute all the taxa ever referred to the families Scylacosauridae, Pristerognathidae, Lycosuchidae, Alopecodontidae, and Ictidosauridae. The bulk of this material is held by the South African Museum in Cape Town, which also houses the largest collection of scylacosaurid therocephalians (approximately 250 specimens) in the world. However, a number of type specimens were also obtained from other institutions, i.e. the Bernard Price Institute for Palaeontology in Johannesburg, the Transvaal Museum in Pretoria, the Macgregor Museum in Kimberley,and the Department of Geology at the Universiy of Stellenbosch. The specimens held by the British Museum of Natural History were studied in London, and those held by the American Museum of Natural History were studied at the University of Chicago where they were on loan at the time. In addition, a number of undescribed specimens were obtained from the collections of the Geological Survey in Pretoria. Specimens which could not be studied at first hand but which were assessed on the basis of the literature were the types of the forms from the USSR, Annatherapsidus, Chthonosaurus, Hexacynodon, Porosteognathus, and Scylacosuchus, which are held by the Palaeontological Institute in Moscow, and the types of the two South African forms Cynariognathus seeleyi

and Pristerognathoides peyeri which are held by the University of Munich.

In spite of some taxa having existed in the literature for as long as 80 years, most of the specimens were poorly prepared because of the extremely hard matrix. In order to assess each specimen as objectively as possible an extensive programme of preparation, which lasted several years and included almost all of the known specimens, was embarked upon and completed. Preparation was predominantly mechanical and because of the hardness of the matrix, carborundom dental burrs were extensively used to remove excess material. Under ideal conditions it was then possible to to reduce the matrix to a thin transparent layer which could be relatively easily removed with vibro-engravers fitted with metal gramophone needles. This method permitted very precise preparation and even the most fragile specimens could be exposed without damaging the original bone surface, when present. Unfortunately the method also generated an enormous amount of fine dust which was not only a health hazard but tended to obscure the area of preparation as well. This problem was resolved by employing light-duty vacuum cleaners and mounting the aperture of the suchtion tube as close as possible to the point of preparation.

A few extremely tough specimens were partially prepared by means of acid according to the method of Rudner (1972). The specimens were coated with a thin solution of polymethylmethacrylate before immersion in acid. In most

instances it was found that the effect of acetic acid on the matrix was so limited that immersion times became excessively long. However, an 11% solution of formic acid proved to be more active and was used instead. The length of immersion in formic acid was determined by inspection but was never more than 24 hours at a time. Care was taken throughout to ensure that no acid penetrated to the surface of the bone.

After each acid bath the specimens were washed in running water for three days and then oven-dried prior to removing the thin layer of etched matrix. Finally, after removal of the covering layer of polymethylmethacrylate, each specimen was coated with a protective layer of Glyptal cement.

In cases where the lack of contrast between the bone and the matrix obscured anatomical detail, specimens were etched with a 10% solution of HCl. The acid was lightly brushed on for 10-30 seconds and rinsed off completely. The bone was then stained red with a solution of Alizarin Red S in a 4% solution of KOH. This technique was also utilised in tracing sutures. An additional advantage of this method is that the specimen can be restored to its original state by re-applying the acid momentarily and then rinsing well.

All preparation was done under stereoscopic microscopes on which the ratio of magnification could be varied between 10 and 40 times.

In order to present as complete a catalogue of illustrations as possible, stereophotographs of all the types and certain selected referred specimens are included in the

descriptive section of the paper. Owing to the poor condition of most type specimens, as well as specific areas which are poorly preserved on most specimens, together with the fact that all specimens are invariably distorted in some way or another, restored drawings of specimens do not always reflect accurately the anatomy of the specimen and may in some cases border on artistic licence.

Stereophotographs are also useful in conveying the actual state of preservation of a specimen as well as any reconstruction which may have been done previously with material such as plaster of Paris. Since the remaining matrix on a specimen is usually omitted in a reconstructed drawing, such an illustration often conveys a false impression of the specimen. The dangers inherent in basing diagnostic features on reconstructed areas of, for instance, skull material, has been amply illustrated by Grine (1981).

The descriptive method employed in this paper to catalogue each specimen is as follows: the specimens are arranged alphabetically according to their most recent taxonomic grouping. Holotypes and referred specimens are indicated, together with the number of each specimen and the institution where it is housed. A brief description of what the specimen consists of is given, together with the state of preservation, the locality and by whom it was collected. An alphabetical list of all taxa with synonyms is included, together with a numerical list of all specimens discussed in the text.

The original generic and specific diagnoses of each specimen are given, and were extracted from the original description of each taxon. Those that have indicated in the original text as diagnoses have been reproduced verbatim. Where the taxonomic diagnosis was not clearly indicated in the text, the original description was scrutinised to determine those features regarded by the original author to have been diagnostic. In all cases however the terminology remains that of the original author. Measurements in millimeters bracketed after tooth numbers in the original diagnoses refer to the habit of earlier authors to record the total distance occupied by those teeth in the jaw.

The localities are given as farm names, followed by the relevant magisterial district. The spelling of some farm names has changed through the years and new names have also come into use as the result of the subdivision of land. In order therefore to avoid possible confusion, Kitching (1977) has been followed throughout in the spelling of the locality names.

Included with each specimen is a list of references indicating where and when the specimen under discussion has been referred to in the literature.

With regard to the components of the strongly heterodont dentition the following convention is applied to the teeth in the upper jaw. All premaxillary teeth are referred to as incisors. Canines are the large maxillary teeth which alternately erupt from either one of two large canine alveoli

in each maxilla. If two canines are present the larger one is termed the funcional one and the smaller the replacement canine (see Van den Heever 1980).

Precanines are the small, possibly non-functional maxillary teeth situated anterior to the canines. All the maxillary teeth situated posterior to the canines are referred to as postcanines. Earlier accounts often incorrectly refer to these teeth as molars as is evident from the original diagnoses of various taxa in the descriptive section. In each lower jaw ramus the large canine is always single. All teeth anterior to the canine are incisors whilst all teeth posterior to it are termed postcanines.

Under the heading of comments the following aspects are discussed:

1. The original generic and specific diagnoses of the specimen in order to determine the validity of its original taxonomic placement.
2. A morphological description of the specimen and where necessary an attempt to correct previous misinterpretations in the light of additional preparation.
3. A short historical discussion of the specimen if its taxonomic placement has been problematical.
4. A new assessment of the validity of each specimen as a separate and distinct taxon in the light of the foregoing.

4. GENERAL COMPARATIVE MORPHOLOGY OF SKULL AND LOWER JAW

1. Introduction

Aspects of the general configuration of the early therocephalian skull and lower jaw have been known since the beginning of this century as the result of Broom's description of Lycosuchus (1903a) and Scylacosaurus (1903c, d). Most of the initial descriptions of early therocephalian cranial material are by Broom and it was also as a result of his insight (Broom 1903b) that these taxa were separated from the rest of the Therocephalia. Most subsequent accounts of the cranial anatomy, especially the earlier versions, have been hampered by the lack of well-preserved specimens as well as preparation techniques sophisticated enough to combat the intractable matrix without damaging the bone. Because of this, descriptive accounts have often been superficial and a large number of taxa, based on non-diagnostic features, have consequently been included in the group by different authors.

A survey of previous diagnoses of the Scylacosauridae reveals a high percentage of non-diagnostic features (see Chapter 2). These include a variety of characters which in some instances are only diagnostic at subordinal level whereas others have also been considered diagnostic only at the specific level. Many are plesiomorphic features which have no

diagnostic value and instead of serving to demarcate, tend to obscure affinities and relationships within and without the group.

The general description of the skull and lower jaw given here was made possible only through further painstaking preparation of the numerous existing specimens in addition to detailed preparation of a number of newly discovered, well preserved skulls. The only region not investigated in detail is the internal aspect of the braincase.

A direct result of this investigation is that it is now once again possible to separate Lycosuchus and its allies from the Scylacosauridae on a large number of features. The two taxa will thus be treated as separate families and will jointly be referred to as the early Therocephalia.

The original diagnosis of the Scylacosauridae (Broom 1903b) was based entirely on plesiomorphic features. Subsequent classifications have fluctuated between the extensive diagnoses of Boonstra (1954a), Von Huene (1956) and Tatarinov (1974) to the more abbreviated versions of Haughton and Brink (1955) and Boonstra (1969b). In order therefore to reassess the diagnostic features of the early Therocephalia it is necessary to consider the general morphology of the skull and lower jaw with reference to previous interpretations.

The skull of the early Therocephalia varies in length. Scymnosaurus, at the upper end of the scale, probably exceeded 400 mm whereas some of the smaller non-juvenile specimens like Scylacosaurus measure approximately 150 mm. The bulk of the

specimens, however, appear to fall between 240-270 mm in length.

Although variation in skull length has been utilised as a diagnostic feature in several previous diagnoses, it is here not regarded as a valid feature because sufficient information concerning growth phenomena within the Therocephalia is as yet lacking. It is not known at present if the early Therocephalia reached skeletal maturity like mammals or whether they underwent continuous growth like reptiles. De Ricqlès (1969, 1976) has suggested that some form of endothermy may have been present in the Therocephalia although additional evidence is still needed with regard to the early Therocephalia. There is some evidence to suggest that turbinals may have been present in the snout of the early Therocephalia but their phylogenetic position, which is close to the base of the Therapsida and the fact that the canines undergo continual alternate replacement, make a reptilian, rather than a mammalian physiology more likely. Moreover, if the above supposition is correct, it would be reasonable to expect that the early Therocephalia exhibited a continuous but differential growth rate, as is common in crocodiles generally. Finally, it is also not yet clear if sexual dimorphism played a size-related role in these taxa.

2. Snout Region

The premaxilla (Figs 1,2,3) forms the terminal portion of

the upper jaw and bears between 5 and 7 incisors. The anterodorsal portion of the bone extends posteriorly as a convex arch, the nasal process, to form the anterior margin of the external naris. The distal portions of the two nasal processes, wedge between the anterodorsal processes of the nasals and terminate at a point in line with the posterior border of the external nares. Posterolateral to the base of the nasal process the premaxilla supports the septomaxilla.

Posterolaterally the premaxilla forms a maxillary process which is covered laterally by the anterior extremity of the maxilla, usually up to the level of the fourth incisor. Posteromedially a vomerine process, which underlies the anterior portion of the vomer, is present in the Scylacosauridae (Fig. 8). In the single lycosuchid where this area has been cleared of matrix it appears that the premaxilla lacks a vomerine process (Figs 9,60b,60e). A similar condition is present in sphenacodont pelycosaurs i.e. Dimetrodon (Romer and Price 1940) and has been suggested for Haptodus (Currie 1979). Whether it is a universal feature amongst lycosuchids must await confirmation since this area is at present inaccessible in the holotype Lycosuchus vanderrieti US D173.

Behind the incisor roots the palatal portions of the premaxillae join to form a flat surface, the premaxillary table, which constitutes the anteriormost portion of the primary palate. The posterior margin of the premaxilla is recessed between the maxillary and vomerine processes to form

the rounded anterior margin of the choana which receives the crown of the lower canine when the jaws are closed (Fig. 8).

Tatarinov (1974) described a single left premaxillary fragment PIN 157/24 (in the figure captions the number is given as PIN 157/23), an alleged pristerognathid from Isheevo, provisionally attributed to Porosteognathus by Vjuschkov (1955). According to Tatarinov (1974) the premaxillary table in this specimen is only slightly emarginated posteriorly. However, in his diagnosis of the family Pristerognathidae the premaxilla is stated as not being posteriorly emarginated by the choana. If this feature were attributed to the Scylacosauridae (=Pristerognathidae) as a whole it would not be concomitant with the condition in the South African specimens which form the bulk of the material.

According to Hopson and Barghusen (1986) a prominent vomerine process, broadly overlapping the ventral surface of the vomer, is a diagnostic feature of the early Therocephalia (their Pristerognathidae) as a whole. They acknowledge that this feature is convergent with the condition found in gorgonopsians. Amongst the Therocephalia, however, it is not restricted to the earlier forms only, but is also present in representatives of other families i.e. Regisaurus, Theriognathus, Moschowhaitsia and Bauria. Forms in which the vomerine process is not visible are the Euchambersiids, a family in which the vomer flares anteriorly (Hopson and Barghusen, 1986), and forms possessing a secondary palate like Scaloposaurus and Ericiolacerta.

A number of foramina are present in the premaxilla. On the lateral surface of the snout, directly below the maxillo-septomaxillary foramen, (=septomaxillary foramen of Watson 1921) the lateral alveolar canal for the superior alveolar nerve (maxillary ramus of V) exits between the maxilla and the premaxilla as the maxillo-premaxillary foramen (Figs 1,2,3,50h). From this foramen a reticulate system of neuro-vascular grooves extend along the alveolar margin of the premaxilla. Watson (1931) described an identical foramen in the advanced therocephalian Ericiolacerta and interpreted it as evidence for the presence of sense organs grouped around the tip of the snout like the mammalian rhinarium. Van Valen (1960) and Estes (1961) pointed out that an equally vascular bone surface is present in the lizard Tupinambis where a rhinarium is absent. In addition Estes (1961) argued that the presence of a large number of foramina on the lower margin of the maxilla actually precludes the existence of a moveable muscular lip and cheek. The presence of these grooves in the early Therocephalia indicate that the integument was closely applied to the bone as in reptiles generally and imply a lack of facial musculature in this region. In addition numerous minute foramina are randomly distributed in the same area.

In sharp contrast to the arborizations along the alveolar rim of the premaxilla, the surface of that portion of the bone which forms the anteroventral corner of the external naris is smooth and lacks both neuro-vascular grooves and foramina. The anterior portion of the septomaxilla which forms the

ventral margin of the external naris (Figs 1,2,3,50g,50h) is also smooth and lacks grooves and foramina. It seems therefore that in this area the integument was not closely applied to the bone and a moveable flap of skin may have been present at the nostril. Kemp (1979) noted a similar condition in Procynosuchus and interpreted it as evidence for the existence of a valvular apparatus controlling the flow of air into the nostril.

Anteriorly, below the base of the nasal process two small apertures, the anterior premaxillary foramina, open as dorsoventral depresssions which link up with the lowermost neuro-vascular groove extending anteroposteriorly along the alveolar rim (Fig. 3). A small opening, the ventral premaxillary foramen, is present on the palatal surface of the premaxilla immediately behind the root of the first incisor (Fig. 8) and another the dorsal premaxillary foramen, in the floor of the external naris directly behind the base of the nasal process. From the latter formen a groove extends upwards along the nasal process for a short distance.

A similar distribution of foramina has been found in the therocephalian Akidnognathus (Brink, 1960), the cynodont Thrinaxodon (Fourie 1974) as well as in the snout of an unidentified gorgonopsian SAM 1125 (pers. observation). In Moschowhaitsia a similar distribution of foramina can be recognised on the premaxilla despite the apparent presence of additional apertures on the dorsal and ventral surface of the bone (Tatarinov 1964, 1974). Fourie (1974) pointed out

similar canals in the higher cynodonts and postulated that the vertical portion of the canal may have been associated with the organ of Jacobson, or a nasal gland with an olfactory function. Kemp (1979) also associated the vertical portion of the canal in Procynosuchus with the organ of Jacobson. According to Kühne (1956) the ventral premaxillary foramen occurs together with the incisive foramen in Oligokyphus and no evidence exists that this small foramen took over the function of the incisive foramen. Kühne considered that the foramen served for for blood supply only, as also demonstrated by Oelrich (1956) in Ctenosaura where the terminal branches of the maxillary artery anastomose at this point. Jollie (1960) showed that the ventral premaxillary foramen is present in most lizards and that its loss is a modification from the more primitive common pattern of lacertilians.

In addition, both Brink (1960) and Fourie (1974) described a canal leading upwards from the ventral premaxillary foramen to the dorsal premaxillary foramen. From this canal a horizontal branch extends anteriorly to open as the anterior premaxillary foramen. Bahl (1937) described an identical configuration in Varanus monitor, which is also present in Varanus albigularis (pers. observation). A single specimen of Varanus niloticus investigated lacked the anterior premaxillary foramen. In Oligokyphus (Kühne 1956) the canal leading from the ventral to the dorsal premaxillary foramen appears not to branch. According to Mendrez (1972b) the dorsal premaxillary foramen is double in Regisaurus and

instead of a ventral premaxillary foramen there appears to be a premaxillary fossa on the ventral surface of the premaxilla into which the ventral premaxillary foramen opens.

From the obvious similarity between the various taxa in the location of the premaxillary foramina, it would seem likely that a similar arrangement of canals existed in the early Therocephalia. However, Tatarinov (1964) maintained that the dorsal premaxillary foramen in Moschowhaitsia has no connection with the ventral premaxillary foramen. He interpreted the ventral premaxillary foramen as giving passage to the terminal branches of the upper incisive artery. Later (1974), he retracted the latter statement and concluded that the ventral premaxillary foramen was the palatal aperture of the nasobasal canal which extends vertically to open close to the midline on the dorsal surface of the premaxilla posterior to the dorsal premaxillary foramen.

Kemp (1979) described foramina in the premaxilla of Procynosuchus which correspond in position to the anterior, dorsal and ventral premaxillary foramina of the forms discussed above. According to him the anterior premaxillary foramen leads into a dorsally directed canal which he presumed to open as the dorsal premaxillary foramen. The ventral premaxillary foramen is said to be linked via a second canal to another foramen situated between the dorsal premaxillary foramen and the septomaxilla, close to the midline on the floor of the nostril. The description of this canal is similar to that given for a similar structure in

Moschowhaitsia by Tatarinov (1974). Kemp (1979) identified this structure as the naso-palatine canal conveying the duct of the organ of Jacobson. However, the presence also of an incisive foramen as well seems to contradict this interpretation.

The septomaxilla (Figs 1-3) is a relatively small bone forming the posteroventral border of the external naris. Anteriorly its thickened base rests on the posterodorsal surface of the premaxilla. The posterior process extends obliquely upwards between the anterior extremities of the nasal and the maxilla as a thin, flat, posteriorly tapering wedge. Anteromedially it forms the medial process which extends inwards as a freestanding, transverse flange within the external naris, dividing it into an anterior and a posterior portion (Figs 1,2,3,50g,50h). The upper rim of the medial process rises towards the midline forming a dorsomedial prong which slightly overhangs a small depression at the base of the process. The two processes from opposite sides of the skull do not meet in the midline and were probably joined by means of connective tissue in life.

The external surface of the posterior process is rugose and matches the surface of the maxilla and the nasal surrounding it. Anteriorly the external surface of the septomaxilla is smooth and unperforated. This indicates that a fleshy appendage, e.g. a moveable nostril, may have been present (Figs 1,2,50g,50h).

A large maxillo-septomaxillary foramen (= septomaxillary

foramen of Watson 1921) is always present on the suture with the maxilla (Figs 1,2,3,50g,50h). Within this foramen a depression is visible on the posterior margin of the septomaxilla (Fig. 2). A groove enters the depression dorsally from the nasal cavity and pierces the septomaxilla as the posterior septomaxillary foramen (Fig. 2). The groove continues anteromedially within the bone as the septomaxillary canal, and exits as the anterior septomaxillary foramen into the depression located anteroventrally on the medial process of the septomaxilla (Figs 2,3).

Brink (1960) described an identical configuration for the septomaxilla in the therocephalian Akidnognathus and pointed out that the general structure of this bone is typical of all carnivorous therapsids but not of the herbivorous Dinocephalia and Anomodontia. In contrast to Brink (1960), Cluver (1971) has stressed the essential similarity between the septomaxillary of the dicynodont Lystrosaurus and that of the therocephalian Akidnognathus. Mendrez (1972b) described and figured a similar configuation of the septomaxilla in Regisaurus. In this form, however, the maxillo-septomaxillary foramen is essentially of a fossa into which two smaller foramina open.

A maxillo-septomaxillary foramen is a distinctive feature of synapsids and is not present in captorhinomorphs or mammals. In pelycosaurs it is bounded by the maxilla, septomaxilla and nasal, except in forms such as Dimetrodon where, as in therapsids, the dorsally expanded maxilla

excludes the nasal. Functionally the aperture has proved rather enigmatic and its presence on the anterolateral surface of the snout has consequently elicited a number of interpretations. Watson (1914a), Simpson (1933) and Cox (1959) regarded it as an exit for the lacrimal duct. However, the lacrimal duct of extant tetrapods does not open to the environment but within the nasal cavity, moistening the nasal mucosa or, as in lizards and snakes, reaches the mouth via the nose to form an addition to the salivary fluid (Romer, 1962). Keyser (1966) has argued that arid conditions periodically prevailed in the Lower Beaufort, and it seems unlikelythat the nasolacrimal duct would have discharged fluid via the maxillo-septomaxillary foramen in animals where the retention of body fluids was probably of importance. Kemp (1969) presented good evidence that in gorgonopsians the nasolacrimal duct opened in the palate and not through the maxillo-septomaxillary foramen.

Cluver (1971) has shown unambiguously that in Lystrosaurus at least, where the lacrimal and septomaxillary bones are in contact, a groove for the nasolacrimal duct extends from the lacrimal canal to the septomaxillary canal. It must, however, be pointed out that the maxillo-septomaxillary foramen in Lystrosaurus is relatively much smaller than in the early Therocephalia.

Watson (1921) reinterpreted the foramen as a structure associated with the flow of air reaching the organ of Jacobson. Unfortunately this novel idea cannot be supported on anatomical grounds. Hartmann-Weinberg's (1938) proposal that the foramen functioned as a passage for saliva from the crown of the lower canine, is patently unfeasible since a canal of this kind would, apart from its unique anatomical disposition, become clogged with food debris.

Romer and Price (1940) were of the opinion that the foramen was too large only to have transmitted vessels and nerves to the surface of the snout. Cox (1959) described a groove on the medial surface of the snout in the dicynodont Kingoria, extending from the medial opening of the lacrimal canal towards the septomaxilla. He was, however, unable to discover its exit. As yet no evidence of a groove for the nasolacrimal duct has been found in the early Therocephalia. This may to some extent be the result of the enormous development of the upper canine, the root of which is enclosed in a large boss on the inner surface of the maxilla, effectively blocking the passage of any duct extending along

the medial surface of the bone towards the anterior portion of the snout. However, in gorgonopsians, where the canine boss is as large as in the early Therocephalia, the groove for the nasolacrimal duct is present behind the canine boss (Kemp 1969).

Tatarinov (1964) proposed that the maxillo-septomaxillary foramen served as an exit for the lateral ethmoidal nerve. By analogy with the condition found in recent lizards he regarded the septomaxillary canal to have given passage to a branch of the same nerve, a suggestion supported by Mendrez (1972b).

Kemp (1969) doubted that the maxillo-septomaxillary foramen was an anterior opening for the nasolacrimal duct because the foramen is absent in mammals indicating that its function in therapsids was no longer required by mammals. Alternatively he proposed that the foramen functioned as a separate air inlet to ventilate the posterior portion of the nasal cavity. According to him the synapsid nasal cavity is much longer than that of captorhinids e.g. Captorhinus, creating an air pocket in the back part which would not be ventilated via the normal route of the respiratory airstream. Because of the improbability of such a condition arising phylogenetically within the Synapsida and then disappearing with the advent of the mammalia this argument is not regarded seriously.

Kemp (1979) showed that Procynosuchus possessed a large septomaxillary foramen. A depression is also present on the inside of the maxilla behind the foramen. He was of the

opinion that the depression contained a mucous-producing gland, the duct of which passed through the maxillo-septomaxillary foramen to the fleshy lips which he also envisaged in this form. Contrary to this interpretation it is also true that the maxillo-septomaxillary foramen is present even in synapsids which certainly did not possess fleshy lips i.e. pelycosaurs and in these forms a different function would have to be attributed to the aperture.

The foramen is too large to have served as the outlet of a single structure. In contrast to the maxillo-premaxillary foramen from which a radiating pattern of grooves extends, the area surrounding the maxillo-septomaxillary foramen is smooth, indirectly indicating that it did not function as a neurovascular outlet (Figs 1,2,3,50g,50h). Alternatively, if a fleshy nostril was present as seems to be indicated by the smooth aspect of the rest of the septomaxila it is possible that this appendage might have extended back to the foramen in which case any neurovascular structures would not have left grooves in the bone.

Brink (1960) related the structure of the septomaxilla to the organ of Jacobson and the function of smell. He argued that with the development of a secondary palate the organ of Jacobson lost communciation with the tongue and became adapted to detecting odours inhaled directly through the nasal cavity. He further stated that a period of time elapsed from when the organ of Jacobson lost communication with the mouth cavity until it readjusted to respond to air inhaled directly into

the nasal cavity. He regarded the peculiar structure of the septomaxilla in the carnivorous therapsids as indicative of such an intermediate period.

This statement is not concomitant with the observed features. Since the development of a secondary palate took place mainlywithin the Therocephalia, the group may be utilized to explain certain features in this respect. The particular configuration of the septomaxilla is standard throughout the group irrespective of the existence of a secondary palate. Even in the early Therocephalia, which possess an essentially reptilian palate with large internal nares, the septomaxilla is identical to that of advanced therocephalia like Ericiolacerta and Bauria which do possess secondary palates.

In cynodonts, where an even more extensive secondary palate is found, the septomaxilla, although smaller, still conforms to the above description. A similar septomaxilla is also found in the pelycosaur Dimetrodon (Romer & Price 1940) and probably in the haptodontine sphenacodont Haptodus (Currie, 1979).

Contrary to Brink (1960), who implied that the development of a secondary palate obstructed the communication between the tongue and the organ of Jacobson, nasopalatine canals pierce the secondary palate in the great majority of mammals, and the ducts of the organ of Jacobson usually open into these canals (Estes 1972).

Certain mammals with functional nasopalatine canals do

possess an additional opening of the vomeronasal organ directly into the nasal cavity (Duvall 1986) and the condition in those mammals which have actually lost the communication between the vomeronasal organ and the mouth (see Estes, 1972 Table 1) can best be explained as an aberration in the palatal structure, e.g. the enlargement of the premaxilla in the horse (Broom, 1896).

Duvall (1986) has pointed out that an incisive foramen is always associated with the secondary palate in mammals and that in fossil forms the appearance of the incisive foramen in conjunction with the development of the secondary palate is therefore significant.

Evidence that the organ of Jacobson retained communication with the oral cavity via the incisive foramen in fossil taxa, despite the development of a secondary palate can be found in forms such as Thrinaxodon, Massetognathus, Probainognathus, Diademodon, Oligokyphus, Bienotherium and Bauria (Duvall, 1986).

The vomeronasal organ in extant reptiles does not communicate with the nasal cavity and the tongue is instrumental in conveying odorants from the environment to within reach of the vomeronasal organ. In mammals the tongue has lost this function but Estes (1972) has suggested a mechanism for introducing odorants into the vomeronasal organs of mammals with functional nasopalatine ducts. By closing both the external nares and the epiglottis, the vomeronasal organ can be ventilated by means of a venturi effect created

by inhaling and exhaling through the nasopalatine ducts. Duvall (1986) has therefore pointed out that the presence of incisive foramina and the associated nasopalatine canals in mammals is a retention of the "mouth smelling function" of the reptilian vomeronasal system during the evolution of the secondary palate.

Brink's (1960) supposition that the organ of Jacobson, after losing communication with the mouth, underwent a period of quiescence and then: "made a bold endeavour to re-establish communication along a different route, the only effective one being through the external nares ...." lacks the principle of physiological continuity and appears to be an unnecessary complication since the organ of Jacobson is a primitive structure amongst tetrapods, has always communicated with the oral cavity in reptiles, and continues to do so in the majority of mammals. Fossil evidence shows that despite the development of a mammal-like secondary palate communication between the vomeronasal organ and the mouth was retained via the incisive foramina.

Consequently the argument by Brink (1960) that the therocephalian septomaxilla is indicative of a period in the evolutionary development of the mammalian condition during which the vomeronasal organ lost contact with the oral cavity and was not yet re-adjusted to detect odour directly through the nasal cavity, is unacceptable.

The maxilla is a large, vertical, plate-like bone which constitutes the greatest portion of the sidewall of the snout

(Figs 1,4). It extends from below the external naris to midway below the orbit and contains the postcanines, canines and in certain taxa, the precanines. On its medial surface a large protuberance, the canine boss, houses the canine alveoli (Figs 2,5,61c,61i,61j). In contrast to its ventral margin which is relatively straight, the bone is sharply convex dorsally to accommodate the roots of the enlarged canines.

Anteriorly, in a very strong contact, the maxilla laterally overlies the premaxilla, usually up to the level of the fourth incisor (Fig. 1). Medially the two bones meet in a zig-zag suture between the last incisor and the anterior canine position. Above and behind the premaxilla, the maxilla forms an oblique suture with the septomaxilla along the posteroventral margin of the latter (Figs 1,50h). Dorsally the maxilla overlies the ventrolateral margin of the nasal. Along its posterior margin it forms an intricate descending suture with the prefrontal, lacrimal and jugal, terminating in a spur, the posterolateral process, midway below the orbit (Figs 1,4).

In palatal view the maxilla forms an extensive contact with the palatine along its entire ventral margin, directly medial to the postcanine tooth row (Figs 8,9). Posteriorly it overlies the lateral margin of the contact between the posterolateral process of the palatine and the anterior process of the ectopterygoid (Figs 8,9). The contact between the maxilla and the palatine then recedes dorsally into a broad, inverted gutter bounded laterally by the posterolateral

process of the maxilla and the anterior process of the jugal, and medially by the anterior process of the ectopterygoid and the posterolateral process of the palatine. This recess receives the oblique anterior margin of the coronoid process when the jaw occludes (Fig. 6).

In the Scylacosauridae a medially projecting maxillary ridge, the crista choanalis is present ventromedially on the canine boss (Figs 8,50c,50d). This feature has been interpreted by previous authors (Mendrez 1972a, Van den Heever 1980) as representing an incipient stage in the development of a bony secondary palate, a structure which develops progressively in certain taxa throughout the Therocephalia. From the available material it appears that a crista choanalis is not developed in the Lycosuchidae (Figs 9,60b,60e,61c,61d,61i,61j) where the inner surface of the canine boss is smoothly rounded. The presence of a crista choanalis is here regarded as diagnostic.

Immediately anterior to the canine boss and a short distance behind the inner aperture of the maxillo-septomaxillary foramen a depression, the anterior maxillary fossa (maxillary depression of Watson 1960) is present on the medial surface of the maxilla (Figs 2,5,61i,61j). Directly behind the canine boss a second depression, the posterior maxillary fossa, lies in a similar position (Figs 2,5,61i,61j). In Lycosuchus GS C60 the latter fossa forms a double pit. Watson (1960) described a similar configuration in certain anomodont taxa and referred to the fossa behind the

canine as the maxillary antrum, as did Cluver (1971) in Lystrosaurus. Kemp (1969) and Tatarinov (1974) referred to the same fossa as the maxillary sinus in gorgonopsians and the therocephalian Moschowhaitsia respectively. In contrast to the above authors Fourie (1974) considered a more posteriorly located cavity lateral to the lacrimo-palatine ridge as the maxillary antrum in Thrinaxodon. This interpretation appears to be at variance with that of the above authors because the same structure is also present in the early Therocephalia and Moschowhaitsia, well behind the posterior maxillary fossa (see description of palatine and lacrimal).

In the early Therocephalia the presence of the two maxillary fossae is the direct result of the extensive medial development of the canine boss and the posterior maxillary fossa may therefore not be homologous with the maxillary antrum of anomodonts. Agnew (1958) established that in the latter the existence of a maxillary antrum is not dependent on the presence of a well developed canine.

The proposal of Kemp (1969) that the posterior maxillary fossa (=maxillary sinus) was filled by a diverticulum of the respiratory passage and probably contained turbinals, appears reasonable and may well have applied to the anterior maxillary fossa as well.

A large maxillo-palatine foramen is present in the palate on the contact between the maxilla and the palatine on the medial surface of the canine boss. In the lycosuchid GS C60 where this area is exceptionally well exposed a second

foramen, more ventrally located, is visiable on the right maxillo-palatine suture. On the left suture the ventral foramen is represented by three smaller openings (Fig. 61j).

The external surface of the maxilla is rugose and, especially in the canine region, covered with a radiating pattern of sulci leading from a large number of foramina (Figs 1,4). A number of alveolar foramina are present on the outer surface of the maxilla, the largest of which is present below the maxillo-septomaxillary foramen. A wide, shallow, anteroventrally directed depression, the preorbital groove, is present on the lateral surface of the maxilla. It extends from the preorbital depression in the direction of the base of the canine crown and the anterior postcanine positions. Boonstra (1954a) used the nature of the preorbital groove as a diagnostic feature at generic level. This depression is, however, universally present in the early Therocephalia as well as amongst the Gorgonopsia and is not considered diagnostic here.

The alveolar canal for the maxillary ramus of V is well developed and is contained within the lower portion of the maxilla. It originates on the inner surface of the maxilla from a large fossa formed by the lacrimo-palatine ridge (Fig. 2) and extends lateral to and above the roots of the postcanines (Figs 61q-t). Anteriorly it passes lateral to the roots of the canines and exits as the maxillo-premaxillary foramen on the lateral surface of the snout directly below the maxillo-septomaxillary foramen (Figs 1,3,50g,50h,61q,61r). A

number of lesser branches extend from the alveolar canal and open as numerous foramina on the lateral surface of the maxilla (Fig. 1). Fourie (1974) described an identical configuration in Thrinaxodon.

The rugose outer surface of the maxilla, especially in the region lateral to the canines, together with the presence of the neurovascular canaliculi, is regarded as positive evidence that the integument was closely applied to the bone and that facial musculature was consequently absent in these areas.

In lycosuchids the postcanines are located on a ventral extension of the maxilla, the ventral maxillary flange (Figs 59c,59d,87a). This structure is separated from the rest of the maxilla by the lateral maxillary ridge (Figs 59c,59d) and may be present as a distinctive plate of bone as in Lycosuchus vanderrieti US D173 and Zinnosaurus paucidens SAM 12185, or less well developed, as in Lycosuchus keyseri GS C60. In contrast, the lower margin of the maxilla in the Scylacosauridae is confluent with the general alveolar margin.

3. Skull Roof

The nasal (Figs 1,2,3) is fairly large and forms the roof of the snout dorsolaterally between the external naris and the frontal. The bone flares anteriorly and forms the dorsal margin of the external naris by means of an anterodorsal process which laterally overlies the nasal process of the

premaxilla. The anteroventral margin of the nasal bounds the external naris posterodorsally, below which it is supported by the posterior process of the septomaxilla in an oblique contact. In the dorsal midline of the snout the nasal forms an extended suture with its opposite number. Ventrolaterally the bone is overlain by the dorsal portion of the maxilla. Posterolaterally the nasal contacts the prefrontal, medial to which it terminates against the frontal in an interdigitating suture.

The general sculpturing of the snout is present over the entire outer surface of the nasal. The inner surface of the nasal is relatively smooth but faint anteroposteriorly directed ridges are present in Glanosuchus macrops GS M796. In Lycedops scholtzi MM 4499 where the undersurfaces of the nasals are preserved as impressions in the matrix, a number of parasigittal ridges and grooves are exposed. Watson (1913) described similar structures in Diademodon and interpreted them as areas of attachment for the turbinal cartilages. Other authors have reached the same conclusion in cynodonts (Brink 1955, Fourie 1974, Kemp 1979), gorgonopsians (Kemp 1969) and dicynodonts (Cluver 1971) and turbinals are now regarded to be universally present in therapsids.

In the Scylacosauridae the nasals are relatively longer than in the Lycosuchidae because of the extended snout of the former. The contact between the nasal and the maxilla therefore extends posteriorly beyond the apex of the maxilla. In dorsal view the impression is thus given that the nasal is

narrow midway along its length and widened posteriorly as the height of the maxilla decreases.

In Lycosuchus vanderrieti US D173 the posterior margin of the nasals is V-shaped, pointing towards the occiput, and in Zinnosaurus paucidens SAM 12185 it appears to be the case as well. In contrast, the posterior margin of the nasals in the Scylacosauridae is expressed as a transverse suture i.e. Glanosuchus macrops GS M796. Although this suture generally appears to be transversely situated in the advanced Therocephalia (Akidnognathus, Olivieria, Bauria) some variation in the pattern does exists. In the Whaitsiidae the suture is usually transverse with the exception of Theriognathus latirostris TM 246 where it is V-shaped, pointing towards the snout (Brink 1980). In Regisaurus (Mendrez 1972b) each nasal terminates posteriorly in a sharp point bounded on both sides by the frontal.

The frontal (Figs 1,4) is a triradiate bone and roofs the skull in the orbital region. Medially it contacts its opposite number in a straight anteroposterior suture in the dorsal midline (Fig. 50k). Anteriorly the anterior process ocntacts the posterior margin of the nasal and is laterally bounded by the prefrontal. The lateral process forms the middle portion of the dorsal margin of the orbit between the prefrontal and the postfrontal. With the exception of some whaitsiids the lateral process of the frontal always contributes to the dorsal margin of the orbit in the Therocephalia as it does in the primitive whaitsiid

Moschowhaitsia (Tatarinov 1974). Boonstra (1954a) concluded that the frontal in the scylacosaurid Scymnosaurus major SAM 9005 was excluded from the orbital margin. Additional preparation of this specimen has shown the statement to be incorrect (Fig. 78b). This condition is also present in some gorgonopsians and all pelycosaurs, with the exception of Eothyris (Romer and Price 1940, Reisz 1980,1986), but not in cynodonts. The posterior process of the frontal lies medial to the postorbital and contacts the parietal in a short, serrate, transverse suture immediately anterior to the dorsal pineal foramen (Figs 59a,63a).

The dorsal surface of the frontal is relatively smooth although the orbital margin may be somewhat thickened and rugose, especially in older specimens (Figs 50k,78b) where the suture between the frontals are often produced as a low ridge. In spite of a certain amount of weathering and distortion it would appear that the interorbital width, expressed as a fraction of the skull length, is greater in lycosuchids than in scylacosaurids.

Ventrally (Figs 7,61n) the frontal is divided anteroposteriorly by a low ridge which forms the dorsomedial margin of the orbit. Lateral to this ridge the lateral process forms the middle portion of the orbital roof and is smoothly confluent with the pre- and postfrontal. Medial to the ridge the undersurface of the frontal is vaulted, forming an inverted gutter with its opposite number. In life this region probably contained the olfactory lobes of the brain.

Kemp (1979) recognised a similar vault in Procynosuchus but pointed out that the depression for the olfactory lobes is incipiently double. In the early Therocephalia this depression is single as appears to be the case in the primitive whaitsiid Moschowhaitsia (Tatarinov 1974) as well.

The presence of an orbitosphenoid is demonstrated by a transverse section through the skull of Lycedops scholtzi MM 4499 where the bone is preserved in situ, and in the skull of Lycosuchus keyseri GS C60 (Fig. 61n) where the possible area of attachment on the undersurface of the frontal is indicated by an anteroposterior groove on the medial surface of the ridge forming the dorsomedial margin of the orbit. A more indistinct groove is present in the same position in the laterally compressed skull of Glanosuchus macrops GS M796 (Fig. 50l). In Lycedops scholtzi MM 4499 the orbitosphenoid appears not to contact the undersurface of the frontal and the connection may have been cartilaginous.

The parietal (Figs 1,12,50a,59a,60a) roofs the skull in the temporal region as a strong median girder extending between the frontal bone and the occipital plate. In lateral aspect it is nearly vertical and forms the inner margin of the temporal fenestra between the postorbital and the squamosal. Anteriorly the parietal contacts the posterior margin of the frontal in a transverse, interdigitating suture and is overlain laterally by the posterior process of the postorbital up to the level of the pineal canal. Posterolaterally a near-vertical, plate-like process of the parietal borders the

temporal fenestra posteromedially and forms the proximal portion of the nuchal crest. Distally this process is wedged between the tabular and the parietal process of the squamosal.

A well developed sagittal crest is always present in the early Therocephalia, arising immediately anterior to the dorsal pineal foramen and terminating in the posterior midline against the nuchal crest.

The vertical pineal canal (Figs 7,61m,61n) is well developed, oval in section and flares towards its ventral aperture. It is situated directly anterior to the epipterygoid-parietal contact. According to Efremov (1940) this structure distinguishes the Therocephalia from all other therapsids and contained the pineal boss of the brain. In contrast to most gorgonopsians, some ictidorhinids and most dicynodonts a preparietal is absent in the Therocephalia.

In section it appears that the parietals are fused in the dorsal midline. However, in the scylacosaurid GS M796 the fusion is further advanced than in the lycosuchid GS C60. Both skulls are of adult specimens but in ventral view the parietals of the former are fused whereas a distinct suture is still present between these bones in the latter (Fig. 61n).

In the fragmentary scylacosaurid GS RS424 (probably Glanosuchus) the parietals are fused except for the portion anterior to the pineal canal where a faint suture line is visible. In Lycosuchus vanderrieti GS M793, a slightly larger lycosuchid, only the area anterior to the ventral pineal foramen could be exposed, but he suture between the parietals

is clearly shown. In the cynodont Thrinaxodon (Fourie 1974) the parietals are fused behind the level of the pineal canal in contrast to the related taxon Procynosuchus (Kemp 1979) where these bones are discrete entities. Whether these observations are taxonomically significant or merely reflect inter-specific variation within the early Therocephalia is not clear at present because of the limited number of adult skulls in which the ventral surface of the parietals are accessible.

Most specimens of early Therocephalia are damaged at the junction between the nuchal and sagittal crests and it is consequently difficult to determine the precise contribution of the parietals to the occiput. In Glanosuchus macrops GS M796 this region, although distorted, is well preserved and it appears that the exposed portions of the parietals are at least equal in surface area to the postparietal and, with the exception of specimens like Regisaurus jacobi (Mendrez 1972b) and Moschorhinus kitchingi (Mendrez 1974), substantially larger than in other therocephalian taxa viz. Ictidosuchops (Crompton 1955) and most whaitsiids (own observation and Brink 1980). In one specimen of Glanosuchus macrops GS M796 the median crest on the postparietal is seen to extend upwards to the parietal suture as it does in the holotype of Ptomalestes avidus SAM 11942 (Fig. 29).

In ventral view the parietals, like the frontals, are vaulted, producing an inverted gutter roofing the brain. Below and anterior to the ventral pineal foramen the vault is widened and deepened across the fronto-parietal suture,

presumably indicating the position of the cerebral hemispheres. In Lycosuchus keyseri GS C60 the anterior portion of the recess is flanked on each side by a low ridge which transects the frontoparietal suture (Fig. 6ln). This ridge appears to be lacking in the scylacosaurid Glanosuchus macrops GS M796.

Posterolateral to the ventral pineal foramen the vault is bounded on each side by a low, ventrally directed, parietal ridge. Lateral to this ridge a sulcus is present in the same position as described in the cynodonts Diademodon (Watson 1920) and Thrinaxodon (Parrington 1946a, Fourie 1974).

It is presumed that the sulcus gave passage to the vena parietalis. This structure extends forward and appears to branch into the orbit along the ventral surface of the frontal (Fig. 6ln)

The head of the epipterygoid contacts the ventral surface of the parietal immediately posterolateral to the ventral opening of the pineal foramen. In the laterally compressed skull of the scylacosaurid Glanosuchus macrops GS M796 the epipterygoid contacts the ventral margin of the ventral parietal ridge (Fig. 50a) whereas in the lycosuchid Lycosuchus keyseri GS C60 the head of the epipterygoid is lodged in a distinct groove medial to the ventral parietal ridge, and is in contact with the medial surface of the latter (Fig 6ln).

4. Circumorbital region

In lateral view the lacrimal (Figs 1,4) is flat and plate-like with its posterior margin forming the middle portion of the anterior border of the orbit. Ventrally it contacts the anterior process of the jugal, anteriorly it forms an oblique interdigitating suture with the maxilla and dorsally it abuts against the ventral margin of the prefrontal. The bone is slightly concave and contains the preorbital depression (Figs 1,39a,40b) from which a wide shallow groove, the preorbital groove (Figs 39a,39b,40b) extends anteroventrally across the lateral surface of the maxilla towards the base of the canine crown. A lacrimal foramen lies within the anterior margin of the orbit.

In medial view the lacrimal forms strong contacts with the jugal, ectopterygoid, palatine, maxilla and prefrontal (Figs 2,5). The contact with the palatine is expressed as a pronounced anteroventrally orientated girder, the lacrimo-palatine ridge, which also forms the anterolateral margin of a large fossa from which the alveolar canal for the maxillary ramus of V originates. Between the lacrimal and ectopterygoid a less pronounced girder, the posteroventrally orientated lacrimo-ecopterygoidal ridge is present. In addition a third structure, the anterior process of the lacrimal (Fig. 2), appears to be present in the Scylacosauridae only. This process is not visible externally and because of a paucity of material in which the internal aspect of the snout is well prepared, it can as yet be seen in 1 specimen only i.e. Glanosuchus macrops GS M796. In this specimen the process is

clearly present on both lacrimals but it appears to be absent in the Lycosuchidae i.e. lycosuchus keyseri GS C60 (Fig. 5). By comparing the two specimens it seems that in the longer snouted Scylacosauridae the anterior process of the lacrimal may serve as a strengthening device.

Between the anterior process of the lacrimal and the lacrimo-palatine ridge the inner wall of the snout exhibits a number of superficial ridges extending anteroventrally onto the medial surface of the maxilla (Fig. 2). It is presumed that these ridges together with the anterior lacrimal ridge as well as those on the inner surface ofthe nasal may have served as areas of attachment for the turbinal cartilages of the snout similar to the ridges found in cynodonts (Watson 1913) and gorgonopsians (Kemp 1969).

The nature of the preorbital depression has been utilized by Boonstra (1954a) as a diagnostic feature at species level. It is present, however, throughout the early Therocephalia and often appears shallow or deep depending on the amount of distortion that the skull was subjected to. In the case of the type of Pristerognathoides minor SAM 3415 the unique nature of the preorbital depression is the result of the technique of preparation (see Chapter 5).

The function of the preorbital depression is uncertain. Brink (1955, 1957, 1978) concluded that the lateral depression on the snout of the cynodont Diademondon contained a gland which secreted a fluid released at the external naris to moisten inhaled air. In contrast Grine et al (1979) regarded this notion as counter adaptive and argued convincingly that the depression contained a salt gland. In Diademodon the depression is situated entirely within the confines of the maxilla and in some cases shallow grooves lead from the depression towards the external naris. In the early Therocephalia the depression is situated further back, on the lacrimal, immediately anterior to the orbit. No foramina have been located opening from within the sidewall of the snout into the depression but this may be as a result of distortion. The surface of the lacrimal within the depression is rugose but not to the same extent as seen on the outer surface of the maxilla in the canine region. This suggests that in life the integument was applied closely to the bone and that on balance the depression probably did not contain glandular tissue.

The prefrontal (Figs 1,4) forms the anterodorsal margin of the orbit. It is a slightly elongated bone with both a dorsal and a lateral face. The lateral face forms part of the sidewall of the snout and contacts the lacrimal and the maxilla whereas the dorsal face forms part of the skull roof and contacts the nasal and the frontal. In lateral view the anterior margin of the bone usually lies in line with the hindmost upper postcanine position.

Contrary to Boonstra (1954a) the prefrontal never ontacts the postfrontal in the early Therocephalia. With the exception of Eothyris (Romer and Price 1940, Reisz 1980,1986) this condition also appears usual in pelycosaurs. In gorgonopsians the contact between the prefrontal and the postfrontal appears to be variable as it is often interrupted by the frontal (see Brink and Kitching 1953a, Sigogneau 1970). A fossa, situated on the medial surface of the prefrontal, overlaps slightly onto the frontal (Figs 7,6ln). This structure appears to be equivalent of the fossa mesethmoidea of Moschowhaitsia (Tatarinov 1974).

The postfrontal (Figs 1,4,7) forms the posterodorsal margin of the orbit and is bounded anteriorly and medially by the frontal, posterolaterally by the postorbital and posteromedially over a short distance by the parietal. It is present in all early Therocephalia and apparently in hofmeyriids (see Hofmeyria atavus Chapter 5) and the Russian form Annatherapsidus petri (Tatarinov 1974) as well. It is absent in the rest of the Therocephalia and in the Cynodontia

but is present in gorgonopsians and pelycosaurs. Its presence is therefore regarded as a primitive feature.

In dorsal aspect the postfrontal is partially overlain by the frontal. The exposed portion is triangular in shape and, especially in mature specimens like Scymnosaurus major SAM 9005 (Fig 78b) and Lycosuchus vanderrieti US D173 (Fig. 59a) rugose with a noticeably thickened outer margin. The ventral surface of the postfrontal forms the posterior portion of the orbital roof and like that of the frontal and prefrontal, is smooth (Fig. 61n). The postfrontal does not contact the prefrotal in the early Therocephalia, some gorgonopsians and most pelycosaurs but see exceptions above.

The postorbital (Figs 1,4,7,61n) is present in all theriodonts an in the early Therocephalia it occupies the upper anteromedial margin of the temporal fenestra. In dorsal view the bone is L-shaped and consists of a latral and a posterior process (Fig. 50k). Proximally the former abuts against the posterior surface of the postfrontal and distally overlaps the dorsal process of the jugal to form a strong postorbital bar, whilst the latter extends posteriorly as a flat vertical sheet against the anterolateral surface of the parietal, terminating at a point in line with anterior margin of the pineal foramen. Proximally the posterior surface of the lateral process forms a rounded depression which served as an area of origin for some of the more anteriorly located fibres of the adductor musculature (Fig. 59f).

Compared with pelycosaurs and gorgonopsians the size of

the postorbital is reduced in the early Therocephalia, especially in the extent of the posterior process. Within the rest of the Therocephalia and Cynodontia the postorbital appears relatively constant and remains comparable in size and configuration with that of the early Therocephalia.

In lateral view the jugal (Figs. 1,2,4,5,50b) is a prominent triradiate element of which the anterior and dorsal processes respectively form the ventral and posteroventral margins of the orbit, and the posterior process forms the anterolateral margin of the temporal fenestra. The anterior process contacts the dorsal head of the ectopterygoid medially (Fig. 2). In lateral view extends forward against and below the ventrolateral surface of the lacrimal, terminating well ahead of the orbit, its ventral margin in contact with the posterolateral process fo the maxilla (Figs. 1,4). Because of this configuration a portion of the anterior process of the jugal is visible in medial view below the ventral margin of the lacrimal. Ventromedially the anterior process of the jugal is excavated (Fig. 6) and, together with the posterolateral process of the maxilla, roofs the wide groove lateral to the head of the ectopterygoid into which the upper margin of the coronoid process of the dentary fits when the jaw occludes. In lateral view the anterior process of the jugal (=suborbital arcade) appears significantly deeper dorsoventrally in lycosuchids than in scylacosaurids. The dorsal process of the jugal contacts the lateral process of the postorbital in an oblique suture that slants upwards and

backwards (Fig. 1). The posterior process of the jugal extends well posteriorly to a point level with the transverse plane of the basal tubera. This process is slender and midway along its length, eillipsoid in section. Posteriorly it is somewhat flattened and applied to the ventromedial margin of the anterolateral process of the aquamosal (Fig. 50b).

5. Palate

The palate in the early Therocephalia has a generally flat aspect with the large anteriorly located choanae, the suborbital fenestrae and the transverse pterygoidal processes as conspicuous well-demarcated features (Figs 8,9). One of the most interesting aspects of therocephalian morphology is the presence of a secondary palate in various stages of development within the group. Initially the early Therocephalia were thought to lack this structure completely, as is evinced by Broom's (1903c) comparison of the early therocephalian palate with that of ".... Rhynchcephalians (sic) and most other primitive reptiles". Mendrez (1972a), however, drew attention to the crista choanalis, a ridge situated along the lateral margin of the internal choana in Pristerognathus. This structure now appears to be universally present in the Scylacosauridae and is interpreted as an incipient stage of the bony secondary palate present in later therocephalians.

The premaxilla has been discussed in a previous section.

The vomer (Figs 8,9,60b) extends between the posterior process of the premaxilla and the anterior margin of the pterygoid. (See description of premaxilla for discussion of contact with vomer). In ventral view the anterior portions of the vomers form a girder which separates the choanae. Posteriorly they expand into a footplate wedged between the palatines and pterygoids. In the early Therocephalia the vomers are unfused as opposed to the Gorgonopsia in which they are completely fused, and the rest of the Therocephalia as well as the Cynodontia (Fourie, 1974) in which these bones are partially fused.

In contrast to other therocephalian groups like the Akidnognathidae (=Annatherapsidae, Euchambersiidae, Moschorhinidae) in which the anterior portions of the vomers are expanded laterally, the vomers in the early Therocephalia are relatively narrow (Figs. 8,9), although appreciably broader than in sphenacodont pelycosaurs like Haptodus and Dimetrodon.

A low ventromedian crest is present on the vomers in the Scylacosauridae. Because of the fragile nature of this structure it is not often seen in prepared specimens. It is, however, present in the holotype of Pristerognathus polyodon BMNH 2581 (Fig. 71a) (Mendrez 1975a, and personal observation), the holotype of Lycedops scholtzi MM 4499 (Fig. 57b), a specimen of Glanosuchus macrops GS M796 and in the serially sectioned skull of a juvenile scylacosaurid SAM K238a (Fig. 28). The crest extends from the anterior margins of the

vomers to the anterior portion of the footplate. That portion of the vomer which forms the medial boundary of the choana has a rounded lateral margin which is expressed as a low ridge on the dorsolateral surface of the bone. Because of this a shallow anteroposterior trough is created on the dorsal surface of the vomer between this ridge and the base of the dorsomedial vomerine crest (Fig. 28). In contrast to the condition in the Scylacosauridae a ventromedian crest on the vomer appears to be lacking in the Lycosuchidae (Figs. 9,60b). In the single lycosuchid specimen in which the vomer is complete and accessible i.e. Lycosuchus vanderrieti GS M793 the vomers anteriorly form a vault (Fig. 9,60b,60e). Whether this feature is diagnostic of the Lycosuchidae as a whole can only be verified with additional well preserved material.

Contrary to Boonstra (1968) the vomers do meet within the snout in a pronounced dorsomedial crest (Fig. 2,28). In the scylacosaurid Glanosuchus macrops GS M796 this structure extends for almost the ful length of the vomers, arising anteriorly as a low ridge and increasing in height up to he contact with the dorsomedial crest of the pterygoid bones (Fig. 2). The dorsal margin of the vomerine crest is damaged in this specimen and it may have been appreciably higher at any point. This is borne out by the condition of the crest in Lycosuchus keyseri GS C60 (Fig. 61d) in which the highest point occurs well ahead of the contact with the pterygoid crest. Along the dorsal margin of this crest the vomers are separated, creating a shallow trough which in all likelihood

supported the cartilaginous internasal septum (Fig. 28). Both Kemp (1969) and Fourie (1974) described a similar vomerine crest and dorsal trough in, repsctively, the gorgonopsian Arctognathus and the cynodont Thrinaxodon.

The palatine (Figs. 8,9,60b) forms a large portion of the palate between the choana and the suborbital fenestra. In contrast to pelycosaurs and gorgonopsians it bears no teeth in the Therocephalia. In the early Therocephalia its anterior portion forms the posterolateral margin of the choana, lateral to the contact with the footplate of the vomer. Laterally it contacts the maxilla in an extended suture directly lingual to the upper postcanine tooth row. A posterolateral process contacts the ectopterygoid anteriorly, forming the anterolateral margin of the suborbital fenestra. Posteromedially the palatine contacts the anterolateral margin of the pterygoid and forms the anteromedial boundary of the suborbital fenestra. The anterior portion of the pterygo-palatine (Figs. 8,9) ridge is present on the posteromedial surface of the palatine.

In ventral view the palatine has a smooth aspect except in the area directly medial to the upper postcanine tooth row, where the lower postcanines bite when the jaws are in occlusion. In sharp contrast to the rest of the bone this portion is distinctly rugose (Fig. 9). The bone is foveate and was probably covred by a layer of keratinised integument as in the horn-covered snouts of dicynodonts. The large posterior palatine foramen (Fig. 9) is situated near the

posterior margin of the bone and from it a sulcus extends anteriorly and posteriorly through the rugose area. A number of foramina are present at the anterior extremity of the sulcus. The posterior portion of the sulcus enters the suborbital fenestra through a groove in its anterior margin (Fig. 9). An additional large foramen is present posterolaterally within the choana on the suture between the palatine and the maxilla (Figs. 5,61j). This foramen corresponds to the "major palatal foramen" of Moschowhaitsia (Tatarinov 1964).

Tatarinov (1964) also reported the presence of a similar rugose surface on the palatine in Moschowhaitsia, a primitive whaitsiid therocephalian which possesses postcanine teeth. He shares the opinion that the area of foveate sculpturing was in life probably covered with keratinised integument. This sculpturing is not present in Theriognathus, a later whaitsiid which lack postcanine teeth. In the latter taxon this area is totally different in that the maxilla forms a ventral shelf behind the canine alveolus so that the anteroposterior maxillo-palatine contact is shifted medially and the palate becomes vaulted. Consequently the lateral portions of the palatine become almost vertical. This area appears to be striated but the intricate arborizations found in the early Threocephalia are absent. A rugose area is also found in the later therocephalian Regisaurus jacobi (Mendrez 1972b). Alhtough not illustrated by that author it is visible on photographs ofthe specimen. This region is absent in the

advanced therocephalian Bauria where the upper and the lower postcanines occlude. The rugose area is therefore present only in specimens with postcanines that do not occlude but bite against the palate medial to the upper postcanine tooth row when the jaws are closed. It is consequently regarded as evidence that a strip of keratinised integument was present on the palatine of the early Therocephalia against which the lower postcanines bit. The fact that this particular structure appears not to be present in the gorgonopsians may indicate a basic difference in jaw function.

Kemp (1969) has described a transverse choanal process on the palatine in the gorgonopsian Arctognathus, which partially divides the nasal cavity. It arises at the front end of the bone and extends high in the snout between the median septum of the vomer and the canine boss of the maxilla. In the early Therocephalia the anterior margin of the palatine also curves upwards, creating a similar but less well developed structure (Fig. 5).

The maxilla has been discussed previously.

The pterygoid bone (Figs. 8,9) is the largest in the palate and constitutes its posterior portion. The anterior pterygoid ramus contacts the palatine posteromedially and the vomer posteriorly. Its lateral edge forms the posterior portion of the medial border of the suborbital fenestra. Just medial to the inner margin of the suborbital fenestra an oblique toothless pterygopalatine ridge is present which anteriorly terminates on the palatine and posteriorly expands

to form the pterygoid boss situated immediately anterior to the proximal portion ofthe transverse process of the pterygoid. In the Scylacosauridae a number of small teeth are present on the pterygoid boss (Figs 8,10) whereas in the Lycosuchidae they are always absent. A single exception to this rule is the type of Trochosuchus acutus SAM 1076. This fragmentary specimen consists of the preorbital portion of a small, possibly juvenile, lycosuchid in which there appears to be root fragments of small teeth implanted in the left pterygoid boss. The transverse process of the pterygoid is roughly triangular, upright and forms the posterior margin of the suborbital fenestra. Its anterolateral surface contacts the ventral process of the ectopterygoid posteriorly (Figs. 9,60b,60d). In posterior view the transverse process ofthe pterygoid is slightly concave. A feature ofthe Lycosuchidae is that teeth are implanted on the ventral margin ofthe transverse process of the pterygoid (Figs. 9,60b). In all scylacosaurids investigated this area is devoid of teeth except in the case of GS RS962 where the roots of a cluster of 4-5 minute teeth are situated proximally on the transverse pterygoidal process immediately lateral to the interpterygoidal vacuity and in the genotype of Lycedops scholtzi MM 4499 where, in the same position, the roots of two small teeth are visible in section (Fig. 57g).

The interpterygoid vacuity is present as an elongated slit situated between the anterior portions of the quadrate rami of the pterygoids (Figs. 8,9). In specimens with

undistorted palates as in Lycosuchus vanderrieti GS M793 this structure is present as a wide opening which originates between the proximal portions of the transverse processes of the pterygoids. Posteriorly the opening narrows markedly, flanked by the ventromedial laminae of the pterygoids which clasp the ventromedial keel of the parabasisphenoid (Fig. 9). Kemp (1979) pointed out that in Procynosuchusthe presence of an interpterygoid vacuity is best interpreted as a remnant of a kinetic mechanism derived from therocephalians and pelycosaurs where this structure is still present. Crompton (1955) concluded that kinetism involving movement of the basipterygoid articulation was present in the skull of Ictidosuchops intermedius. In the early Therocephalia the structure of this area appears to preclude movement of this kind.

The quadrate ramus of the pterygoid sweeps posterolaterally and contacts the posteromedial surface of the quadrate above the contact of the latter with the stapes (Fig. 8). Anteriorly the ventral surface of the ramus is gutter-shaped and, with its fellow, encloses the tear-shaped interpterygoid vacuity. They clasp the anterior portion of the median parabasisphenoid forming the anterior portion of the ventromedian parabasisphenoid keel immediately behind the interpterygoid vacuity. The foramen for the internal carotid is visible at the base of the keel on the suture between these two bones (Fig. 9,6lu). Posteriorly the roof of the quadrate ramus is absent and the bone extends posterolaterally as a

thin vertical lamina towards the quadrate. Dorsally the quadrate ramus of the pterygoid supports the base of the epipterygoid (Figs. 12,60d).

The dorsal aspect of the pterygoid is interesting in that it forms, with its fellow of the opposite side, a thin, high lamina in the midline of the snout, extending posteriorly from the contact with the vomerine septum to the level of the orbit (Figs. 50d,61d). Boonstra (1968) found only a low dorsal septum in the single, possibly juvenile scylacosaurid specimen which he studied. He also indicated that the upper margin of the pterygoid septum formed a trough posteriorly above the interpterygoid vacuity. Immediately lateral to the base of the pterygoidal lamina a smooth wide trough is present. Behind the base of the dorsal lamina of the pterygoid in Lycosuchus keyseri GS C60 the interpterygoidal vacuity opens dorsally in a trough extending from the base of the pterygoidal lamina to the base of the cultriform process of the parasphenoid. Lateral to the interpterygoidal trough the thickened dorsal surface of the pterygoid is excavated to form a lesser groove.

The ectopterygoid, (Figs. 2,5,9,60b,60d) situated lateral to the suborbital fenestra, is a narrow, vertical strut with three processes. The ventral process is applied to the anterolateral margin ofthe transverse pterygoidal process forming a lateral face against which the medial surface of the lower jaw abuts when adducted. The anterior process extends forward and slightly downward to contact the posterolateral

processes of the maxilla and the palatine forming the posterolateral margin of the suborbital fenestra. The dorsal process supports the suborbital bar ventromedially at the lacrimo-jugal contact, forming a suture with both these bones.

6. Temporal region

The structure of the temporal region in the Therocephalia is significant in that it is the most primitive taxon where the broad skull roof and small temporal fenestrae of the earlier therapsids are replaced by a narrow intertemporal region and large temporal fenestrae. This configuration not only reflects probable changes in the architecture of the adductor musculature but also indicates a level of evolutionary development approximating the phylogenetic position of the Cynodontia, and ultimately the Mammalia, more closely than any other non-cynodont therapsid taxon.

In the early Therocephalia the squamosal (Fig. 1) forms the posterior wall of the temporal fenestra and in agreement with Brink (1956), Mendrez (1972b,1974) and Kemp (1972a) can be described in terms of its processes. A dorsal process contacts and overlies the parietal posterolaterally. Below this contact an intermediate process meets the supraoccipital and the pro-otic (Figs 1,12). A quadrate process covers and supports the quadrate and the quadratojugal from behind (Fig. 20) and, anterolaterally, the zygomatic process extends outwards and forwards to overlie the posterior process of the jugal, forming a slender zygomatic arch (Fig. 50b)

A fifth process which contributes to the formation of the pterygo-paroccipital foramen is present in the advanced Therocephalia and the Cynodontia. This foramen is formed by a

slender bar, horizontally bridging the anterior opening of the posttemporal fenestra. Both the prootic and the squamosal contribute processes to this structure. Kemp (1972a) has summarised the distribution of the foramen in synapsids, pointing out that the otic process of the squamosal and the lateral process of the prootic, by which the above foramen is formed, are lacking in eotheriodonts, pelycosaurs, gorgonopsids and dicynodonts. Up to now the presence of a pterygo-paroccipital foramen, although suspected, has not been definitely demonstrated in the early Therocephalia. As a result of this investigation it is now evident that a pterygoparoccipital foramen is at least present in the Scylacosauridae (Fig.12). No indication could be found in the available material of the presence of a similar structure in the Lycosuchidae. This would indicate a possibly closer relationship between the Scylacosauridae and the rest of the Therocephalia than between the former and the Lycosuchidae. However, compared with the rest of the Therocephalia the anatomy of the pterygoparoccipital region in the Scylacosauridae does appear different from the rest of the Therocephalia to some extent. The otic process of the squamosal projects medially as a flat, convex sheet of bone completely covering the anterior opening of the posttemporal fenestra. Because of this the dorsal and ventral openings of the pterygoparoccipital foramen are offset. The dorsal opening is present as a relatively small, medially placed aperture whilst the large ventral opening is more laterally

placed, just medial to the head of the quadrate. It would appear that the structure described above served to protect neurovascular elements passing through the posttemporal fenestra. Medially the otic process of the squamosal contacts the lateral process of the prootic. It is not possible to determine exactly from the available material what the contribution of each bone is, but it appears that the squamosal contributes the greater part (Fig. 12). In Regisaurus (Mendrez 1972b), Moschorhinus (Mendrez 1974) and Whaitsia (pers. obs.; Kemp 1972a) the otic process of the squamosal does not form as extensive a sheet as in the Scylacosauridae and its distal portion is therefore rod-like. Consequently the dorsal and ventral openings of the pterygo-paroccipital foramen are dorsoventrally in line in these taxa

On the posterolateral surface of the squamosal a broad, dorsoventral sulcus is present, medially bordered by the prominent squamosal ridge (Figs 29,30,59e). The existence of this structure in the early Therocephalia has been known since the turn of the century (Broom 1903a) and has subsequently been described in other therapsids as well. From its position and development the conviction grew that it was associated with an external acoustic meatus. However, Allin (1975) proposed that the structure functioned only as an area of origin for the m. depressor mandibulae.

In the carnivorous therapsids the size of the lower jaw is such that the m.depressor mandibulae need not have been a large muscle, a view supported by the relatively small size of

the retroarticular process of the articular. In contrast, the squamosal sulcus is much more well developed than would be expected of the area of origin for a small muscle. In addition, the complex tubular nature of this structure in some of the more advanced therapsid taxa e.g. Diademodon, corroborates this interpretation, and makes it difficult to reasonably ascribe any other function than acoustic to the region. Later, Allin (1986) adapted his previous interpretation and currently supports the contention that the therapsid squamosal sulcus contained an external acoustic meatus.

Posterodorsally the squamosal is covered by the tabular. Posteroventrally the squamosal meets the mastoid head of the paroccipital process in a strong contact. Lateral to this the ventral margin of the squamosal is gently emarginated before it descends as the quadrate process behind and against the dorsal portion of the quadrate and the upper part of the quadratojugal (Fig. 20).

Broom (1936c) called attention to the cleft appearance of the posteroventral margin of the squamosal in the holotype of Lycedops scholtzi MM 4499 (Figs 57e, 57f). This specimen is extensively weathered over its entire outer surface (see Chapter 5) and the cleft ventral margin of the squamosal may in part be the result of damage. Both the quadrate and the quadratojugal fit side by side into a recess in the anteroventral surface of the squamosal and are consequently covered posteriorly by a relatively thin sheet of squamosal.

Because those portions of the squamosal which abut against the quadrate and quadratojugal fit into depressions on the posterior surfaces of these bones they are more resistant to weathering than the narrow unsupported portion of squamosal between them. Consequently the right amount of weathering will produce a cleft between these bones. This is borne out by the fact that in the holotype of Lycedops scholtzi MM 4499 the posterodistal portions of the squamosals are largely present as impressions and those portions of the squamosal that are preserved lie against the quadrate, the quadratojugal and the mastoid head of the paroccipital process. In addition Kemp (1972a) has commented on the general lack of a cleft squamosal in the Therocephalia, except in the holotype of Lycedops scholtzi and the Whaitsiidae. His interpretation of the squamosal of Lycedops was based on the description of Broom (1936c) and although it seems that some form of a cleft squamosal may have been present in the early Therocephalia. As Crompton (1972) demonstrated the presence of prominent clefts in the ventral margin of the cynodont squamosal, additional well preserved material is needed to clarify the morphology of this region in the early Therocephalia.

Anteroventrally the squamosal is recessed to receive the dorsal portions of the quadrate and the quadratojugal (Fig. 32). The recess is wide at the lower margin of the squamosal and narrows markedly towards the top. The posterior and lateral walls follow the contour of the squamosal but the lower half of the inner wall is produced as a triangular,

anteroposteriorly directed face. The apex of the triangle points dorsally and the whole surface inclines laterally at an angle of approximately 30 degrees to the vertical. The medial face of this surface contacts the dorsal portion of the quadrate head of the paroccipital process.

The quadrate (Figs 11,12,20,29) consists of a dorsal body, imbedded in the squamosal recess and a ventral, transversely elongated roller which articulates with the lower jaw. Several distinct features are present on the quadrate. In posterior view the body is dorsally embayed to receive the ventrally directed quadrate process of the squamosal (Figs 11b, 20). The lateral and medial margins of this depression is produced as prominent ridges. The lateral ridge projects towards the quadratojugal (Fig. 11a,b) and is situated in a similar position as the quadrate flange described by Crompton (1972) in the cynodont Thrinaxodon. The ventrolateral portion of the body of the quadrate is emarginated and forms the medial border of the quadrate-quadratojugal foramen (Fig. 11b). Dorsal to the foramen the lateral surface of the quadrate is grooved to receive the dorsomedial margin of the quadratojugal (Fig. 11a). The anterolateral margin of the quadrate forms a sharp dorsoventral ridge. In anterior view, within the temporal vacuity, the body of the quadrate is broad, concave and almost square in outline. Anteromedially where the anterior and medial faces of the quadrate meet the bone is produced as a prominent dorsoventral crest, the lower portion of which extends anteromedially for a short distance

as the pterygoid process to contact and laterally overlie the distal extremity of the quadrate ramus of the pterygoid (Fig. 12).

The medial face of the body of the quadrate is anteroposteriorly widened and slightly concave. The upper portion of this face lies against the medial wall of the quadrate recess in the squamosal. The lower portion of this face forms a strong contact with the quadrate head of the paroccipital process (Fig. 20).

The quadrate roller (Fig.12) possesses a lateral and a medial condyle similar to that described in gorgonopsians (Parrington 1955) and whaitsiids (Kemp 1972b). The lateral condyle has the larger surface and extends forward onto the anterolateral surface of the roller which in turn abuts against a near vertical anterior extension of the articular glenoid (Fig.23a). This arrangement facilitates a wide gape, and upon adduction of the lower jaw, prevents posterior dislocation. A similar feature has been recorded in Scymnosaurus ferox (Boonstra 1953c).

Dorsolaterally the roller supports the base of the quadratojugal (Fig. 11b) whilst medially it contacts the distal head of the stapes. Contrary to Boonstra (1953c) no indication of a definite facet to receive the stapes was found.

The quadratojugal is a vertical splint-like element resting on the dorsolateral surface of the quadrate roller (Fig. 11b). Above its slightly widened base the bone is

medially emarginated to form the lateral wall of the quadrate-quadratojugal foramen. Above this foramen its inner margin is rounded and fits into a vertical groove on the dorsolateral surface of the quadrate (Fig. 11a). This configuration differs from that found in whaitsiids by Kemp (1972b) where the lateral margin of the quadrate lies in a groove on the quadratojugal. A depression into which the squamosal fits is present on the posterior surface of the quadratojugal above the level of the quadrate-quadratojugal foramen (Fig. 11a). This structure is similar to that found on the quadrate and served to strengthen the contact with the squamosal.

The jugal and postorbital has been discussed earlier.

7. Braincase and occiput

The internal anatomy of the braincasedoes not form part of this investigation and only the outer aspect will be discussed. Previous descriptions of the early therocephalian braincase include that of Haughton (1918), Broom (1936c), Olson (1938a) and Boonstra (1934, 1954a, 1968). The contribution on the early therocephalian braincase by Olson (1944) will not be considered since Van den Heever and Hopson (1982) have shown that his description of "therocephalian B" was based on the skull of a gorgonopsian.

In the early Therocephalia the lateral wall of the braincase is formed by the prootic, opisthotic and

supraoccipital, the floor is formed by the basioccipital and parabasisphenoid and the roof by the parietal. The posterior wall is formed by the exoccipital. The isolated position of the epipterygoid with respect to the prootic is reminiscent of the condition found
in gorgonopsians, but the bone is specialised in that it is anteroposteriorly widened.

The prootic (Figs 1,4,12) forms the anterolateral portion of the sidewall of the braincase. Anteriorly it contacts the epipterygoid, dorsally the supraoccipital, posterolaterally the squamosal, posteroventrally the opisthotic and ventrally the basisphenoid portion of the parabasisphenoid. Contrary to Olson (1938a) the early Therocephalia do not possess a periotic since a suture, separating the prootic and opisthotic, extends ventrally between the fenestra ovalis and the ventral opening of the pterygo-paroccipital foramen (Fig. 8). Crompton (1955) suggested the presence of a periotic in Ictidosuchops intermedius but Mendrez (1972b,1974), on the other hand, clearly demonstrated the existence of a distinct prootic and opisthotic in forms such as Regisaurus and Moschorhinus, respectively. Boonstra (1968) figured the skull of a possibly juvenile early therocephalian with distinct sutures between these bones.

Ventrally the prootic contacts the basisphenoid in a jagged suture which extends from the dorsum sellae to the anterior margin of the fenestra ovalis (Fig. 4). Anteroventrally at this contact the prootic forms the dorsal

portion of the transversely placed dorsun sellae (Fig. 12). Careful staining of this structure and the sella turcica has revealed that Boonstra (1968) was correct in stating that the two medial processes of the prootics which contribute to the dorsum sellae, closely approximate one another in the midline but do not actually meet. Later, Boonstra (1971) stated that these bones just meet in the midline. Lateral to this structure the elongated anteroventral process of the prootic extends anterodorsally. This process is most often damaged and its exact length is consequently unknown. However, in a new specimen of Glanosuchus macrops, GS M796, it appears complete in the left half of the skull and is present as a thin, distally spatulate rod equal in length to the vertical height of the epipterygoid (Fig. 50f). In this specimen the distal extremity of the anteroventral process contacts the epipterygoid dorsomedially. This may not be a true reflection of the anatomy since the skull is laterally compressed. A short distance posterior to the base of the anteroventral process the foramen for the seventh cranial nerve pierces the sidewall of the braincase (Fig. 4). Partially surrounding the foramen is a shallow pit which presumably contained the geniculate ganglion. Immediately above the anteroventral process a deep cleft, the incisura prootica is present. Dorsal to the incisura prootica the anterodorsal process of the prootic extends forward and upward, parallel to the anteroventral process, to contact the epipterygoid dorsomedially (Fig. 4). In Ptomalestes avidus SAM 11942 where

the braincase is virtually undistorted, the anterodorsal process is partially wedged between the epipterygoid and the supraoccipital at their point of contact.

The lower portion of the prootic is essentially a vertical plate. Dorsolaterally, however, the bone extends inwards towards the supraoccipital and forms a shelf in the posteromedial corner of the temporal vacuity. Posterolaterally, just below this shelf the lateral process of the prootic meets the otic process of the squamosal. This structure bridges the anterior opening of the posttemporal fenestra and its significance has been pointed out earlier in the discussion of the squamosal (Fig. 12).

An interesting feature, observed only in Ptomalestes avidus SAM 11942, is a small prootic process situated ventromedially to the lower opening of the pterygo-paroccipital foramen. The dorsal surface of this structure appears concave and it is reasonable to suspect that it may have supported neurovascular elements passing along the outer surface of the braincase.

Posteroventrally the prootic forms the anterodorsal margin of the fenestra ovalis

The opisthotic (Figs 8,29,30) forms a strong, transverse girder between the braincase and the suspensorium. Anteriorly it meets the prootic. Ventromedially it contacts the basioccipital and the prootic to form the posterodorsal border of the fenestra ovalis. Posteromedially it forms the lateral border of the large jugular foramen above which it contacts

the exoccipital and extends upward as the dorsal process to meet the supraoccipital medial to the posttemporal fenestra. Distally it forms a quadrate and a mastoid head, the former contacting the medial surface of the quadrate and the posterior extremity of the quadrate ramus of the pterygoid, and the latter contacting the squamosal medial to the ridge which forms the medial border of the squamosal sulcus. Ventrodistally a deep, oval fossa is present between the two heads (Fig. 20). In posterior view the ventral margin of the posttemporal fenestra is formed by the dorsal surface of the paroccipital process (Fig. 29,30). This area is smooth in the early Therocephalia and lacks a posttemporal fossa which is a feature of the advanced Therocephalia. The lack of a posttemporal fossa cannot, however, be utilised to group the the Scylacosauridae and the Lycosuchidae since it is a plesiomorphic feature.

As in other early therocephalians the squamosal extends laterally to cover the quadrate and quadratojugal posteriorly (Fig. 11b). The quadrate and quadratojugal are situated in a depression on the anteroventral surface of the squamosal (Fig. 32). The contact between these bones and the squamosal seems relatively loose.

The epipterygoid (Figs 1,4,12,32), although anteroposteriorly widened beyond the gorgonopsian condition, is not closely associated with the prootic as in later therapsids and a cavum epiptericum is still present. Compared with the rest of the taxon, the the early therocephalian

epipterygoid exhibits the least amount of anteroposterior widening and consequently represents the most primitive condition of this structure amongst the non-gorgonopsian theriodonts of South Africa. It has a standard configuration and differs considerably from that of pelycosaurs and gorgonopsians.

The bone is plate-like and extends vertically from the quadrate ramus of the pterygoid to contact the ventral surface of the parietal, just posterior to the plane of the parietal foramen. In lateral view it is hour-glass shaped in that it is anteroposteriorly widened both dorsally and ventrally with a narrow middle portion. Dorsally the head of the epipterygoid fits into a groove on the underside of the parietal, just behind the ventral opening of the pineal canal and directly medial to the ventrolateral rim of the parietal. (See discussion of the ventral surface of the parietal for differences in the epipterygoid-parietal contact between Glanosuchus macrops GS M796 and Lycosuchus keyseri GS C60.)

In both Glanosuchus macrops GS M796 (Fig. 1) and Ptomalestes avidus SAM 11942 the epipterygoid is dorsomedially contacted by the anterodorsal process of the supraoccipital. Directly below this contact the anterodorsal process of the prootic meets the inner surface of the epipterygoid. Ventrally the bone is widest and forms an anterior and a posterior process resting on the quadrate ramus of the pterygoid (Fig. 1). The anterior process is medially thickened and appears to extend towards the region of the

basipterygoid process. In Regisaurus the epipterygoid apparently possesses a posterior apophysis which, according to Mendrez (1972b), probably separated the maxillary and mandibular rami of the trigeminal nerve. This structure has not been observed in the early Therocephalia, where both the anterior and posterior margins of the bone are smooth. According to Boonstra (1934) the epipterygoid of Trochosuchus major BMNH R5747 differs from that of Scylacosaurus in that it is widened and resembles that of cynodonts, a point mentioned also by Barry (1965). However, in the light of additional information it can now be seen that the epipterygoid of this specimen conforms to the general configuration for the early Therocephalia (see Trochosaurus major BMNH R5747 Chap. 5).

The parabasisphenoid is a median element in which the suture between parasphenoid and basisphenoid cannot be externally determined. Anteriorly the bone is immovably clasped between the quadrate rami of the pterygoids, dorsally it forms a strong interdigitating suture with the base of the prootic, posteriorly it meets the basioccipital in an equally strong contact and ventrally it forms the posterior portion of the deep ventromedian keel.

Anterodorsally just behind the contact with the pterygoids a freestanding, needle-like cultriform process extends anterodorsally, overhanging the dorsal opening of the interpterygoid vacuity. Boonstra (1968) found this process inclined upwards at an angle of 30 degrees to the horizontal in a scylacosaurid studied by him. One scylacosaurid and one

lycosuchid skull in which the cultriform process is incompletely preserved was available for this investigation. It appears that the angle of the cultriform process of the scylacosaurid agrees with the observation of Boonstra (1968), whereas the process appears to be angled at approximately 60 degrees to the horizontal in the lycosuchid. Since a certain amount of distortion is present in most specimens this difference cannot be regarded as a diagnostic feature unless substantiated by additional material. The dorsal surface of the cultriform process is longitudinally grooved and it presumably served as support for a portion of the sphenoid complex. The cultriform process is damaged in all specimens investigated so that its full extent could not be determined. Boonstra (1968) figured the sectioned skull of an early therocephalian in which the length of the rostrum approximated the combined length of the parabasisphenoid and basioccipital in ventral view.

The basipterygoid process is short and stout. The contact with the quadrate ramus of the pterygoid is strong and it is clear that a moveable basipterygoid articulation was not present.

Posterodorsally the parabasisphenoid forms the lower portion of the dorsum sellae as was also pointed out by Boonstra (1968). The sella turcica is present as a shallow depression medially divided by a low, median ridge in the scylacosaurid Glanosuchus macrops GS M796. In the holotypes of the scylacosaurid Ptomalestes avidus SAM 11942 and the

lycosuchid Lycosuchus keyseri the sella turcica appears not to be divided. In both the scylacosaurids Ptomalestes avidus SAM 11942 and Glanosuchus macrops GS M796 the sella turcica appears better defined than in the lycosuchid Lycosuchus keyseri GS C60. In addition the lateral margins of the sella turcica form sharp ridges in the former two specimens whereas the same area is bluntly rounded in the latter. Until such time as more material is available these apparent differences will not be regarded as diagnostic.

Posteriorly the parabasisphenoid flares to form the basal tuber. This structure contributes to the anteroventral margin of the fenestra ovalis and posteriorly contacts the basioccipital. In the Scylacosauridae the basal tubera are small and the basicranial axis narrow in the region of the foramen for the internal carotid, immediately anterior to the tubera (Fig. 8). In the Lycosuchidae, on the other hand, the tubera are much larger and the basicranial axis is more robust (Fig. 9). The size of the basal tubera are important since they serve as areas of insertion for portions of the ventral neck musculature. This feature is quite distinct in all specimens investigated and is consequently regarded as diagnostic.

Ventrally the parabasisphenoid forms the posterior portion of the deep, ventromedian keel whereas the pterygoid comprises the anterior portion. At the base of the keel the foramen for the internal carotid bridges the suture between these bones (Fig 61u). In Ptomalestes avidus SAM 11942 the

canal for the internal carotid joins its opposite number as they pass upwards through the parabasisphenoid. In Lycosuchus keyseri GS C60 a large, unpaired foramen is situated dorsomedially behind the base of the cultriform process of the parasphenoid. A second foramen is assymmetrically located immediately anterolateral to the base of the cultriform process, posterolaterally within the groove that forms the dorsal opening of the interpterygoid vacuity. Romer and Price (1940) have described a similar condition in pelycosaurs and were of the opinion that the posterior opening emitted the pituitary artery and the anterior opening carried the joint carotids. Contrary to the condition found in pelycosaurs it appears to be the anterior foramen which is assymmetrically located in the early Therocephalia

The parietal has been discussed earlier.

The basioccipital (Figs 8,9) is a short, stout bone which forms the hindmost portion of the skull base. Anteriorly it meets the posterior margin of the basisphenoid in a jagged suture between the basal tubera. In ventral view the bone is concave because a lateral process (Fig. 9) extends downwards on each side, contributing to the posteroventral margin of the fenestra ovalis and contacting the proximal portion of the paroccipital process of the opisthotic. Posteriorly the bone meets the exoccipital to form the lower half of the tripartite occipital condyle (Figs 29,30). In occipital view a small portion of the basioccipital is visible between the condyle and the short ventrolateral spur of the exoccipital. In the

holotype of Lycosuchus keyseri GS C60 a small area of cancellous bone is present on the ventral midline at the suture between the basioccipital and the basisphenoid. This feature corresponds to the unossified zone mentioned by Olson (1944) and Fourie (1974) and appears to be generally present in therapsids. A pair of small foramina is situated on the ventral midline just behind the unossified zone.

The therocephalian occiput is broad and low (Figs 29, 30). In contrast to the Pelycosauria (Haptodus, Dimetrodon) and the Gorgonopsia (Gorgonops, Hipposaurus) where the occipital plate exhibits a marked forward slant, this region has a vertical aspect in the Therocephalia. The upright nature of the occiput is almost certainly the result of the emargination of the intertemporal region to accommodate the adductor musculature. Although the various occipital elements appear to have a constant configuration throughout the group, a striking feature of the early therocephalian occiput is the radial pattern of structural reinforcement around the foramen magnum. Dorsomedially the parietals and squamosals join in a strong nuchal crest which is supported ventrolaterally on each side by two broad tabular ridges, angled at approximately 45 degrees to the horizontal. Ventrolateral to the foramen magnum the robust paroccipital processes extend laterally to contact the squamosal and quadrate. Between the tabular ridge and the paroccipital process a large posttemporal fenestra is present.

The postparietal (Figs 29,30) is a single median element

dorsally bounded by the exposure of the parietal on the occiput, ventrally by the supraoccipital and laterally by the tabular. The bone is situated within a large occipital depression. A low, median ridge which extends vertically from the supraoccipital to the occipital portion of the parietal divides the depression into two nuchal fossae. These structures, high on the occiput, indicate areas of attachment for the dorsal neck musculature. From the available material it appears that the occipital depression of lycosuchids is more pronouced than that of the scylacosaurids (Figs 29,30). In one specimen of Glanosuchus macrops GS M796 a small portion of what appears to be the postparietal is present high on the sidewall of the braincase between the parietal, anterodorsal process of the squamosal and the anterior process of the supraoccipital (Fig.1).

In posterior view the supraoccipital (Figs 29,30) is dorsally bounded by the postparietal and laterally by the tabular. Ventromedially it contributes to the dorsal margin of the foramen magnum over a short distance and, lateral to that, forms sutures with the exoccipital and the dorsal process of the opisthotic. The anterodorsal process of the supraoccipital extends forwards and upwards below the postparietal to contact the parietal, squamosal, prootic and epipterygoid (Fig. 1). Olson (1938b) pointed out that in the gorgonopsian Cynariops the supraoccipital forms the dorsal margin of the foramen magnum as well as a portion of the dorsal skull roof. Whether this is true of the early

therocephlians is uncertain. In occipital view it appears that the supraoccipital forms the dorsal portion of the posterior braincase wall. In the holotype of Ptomalestes avidus SAM 11942 where the braincase has been freed of matrix internally the supraoccipital is seemingly excluded from this position since internally a midline suture appears to extend the length of the braincase roof to terminate close to the dorsal margin of the foramen magnum. It would appear therefore that the contribution of the supraoccipital to the roof of the braincase is limited.

Within the temporal vacuity the anterodorsal process of the supraoccipital contributes to the sidewall of the braincase. In Glanosuchus macrops GS M796 this feature is visible on both sides of the skull (Fig. 1). Anteriorly it meets the dorsomedial surface of the epipterygoid, dorsally the parietal and postparietal, laterally the squamosal and ventrally the prootic. This configuration is similar to that found by Broom (1936c) and Boonstra (1968) in early therocephalians and by Mendrez (1974) in Moschorhinus. Boonstra (1968) pointed out that a gap, present in his specimen between the prootic and the supraoccipital, indicated that his specimen was a juvenile. This gap, albeit smaller, is also present in mature specimens i.e. Glanosuchus macrops GS M796. What appears to be a suture is present at the base of the dorsal notch in this specimen (Fig. 1), indicating that the prootic does not extend dorsally beyond this point. According to Mendrez (1974) a dorsal lamina of the prootic is

present behind the dorsal notch in Moschorhinus. Glanosuchus macrops GS M796 has been laterally compressed and the alleged suture at the base of the dorsal notch may be an artefact. However as evinced by this specimen it seems that the sheet of bone directly behind the dorsal notch consists of supraoccipital only (Fig 1). The condition in Ptomalestes is similar and appears to substantiate this interpretation.

The exoccipital (Fig. 29,30) forms the lateral margin of the foramen magnum as the dorsolateral portion of the tripartite condyle. A long lateral process lying proximally against the posterior face of the paroccipital process forms the dorsal margin of the large jugular foramen. A short ventrolateral spur forms the medial and ventromedial margin of the jugular foramen. The lateral margin of the jugular foramen is formed by the paroccipital process. Boonstra (1968) included the exoccipital as part of the lateral wall of the braincase but the exposure of this bone is so small that it really only contributes to the posterior wall.

The tabular (Fig. 29, 30) is a relatively large bone located dorsolaterally on the occiput. It supports the squamosal from behind and forms the angled tabular ridge between the foramen magnum and the posterodorsal rim of the temporal fenestra. The ventral margin of the tabular invades the dorsolateral portion of the posttemporal fenestra and sends a short ventrolateral spur along the inner face of the ridge forming the medial border of the squamosal sulcus (Fig. 30). The lateral and most of the dorsal border of the

posttemporal fenestra is formed by the squamosal. Dorsomedially the posttemporal fenestra is bordered by the dorsal process of the opisthotic, which excludes the tabular from that position (Fig. 30). The fenestra is floored by the dorsal surface of the paroccipital process. In contrast to the rest of the Therocephalia, no paroccipital fossa is present in the early Therocephalia.

The squamosal has been discussed earlier. In posterior view it forms the lateral portion of the occiput on which the vertical squamosal sulcus features prominently.

8. Stapes

The stapes has been described in a number of therocephalian taxa (Broom 1936c, Brink 1963, Boonstra 1934, 1953c, 1954a, Sigogneau 1963, Cys 1967, 1971, Mendrez 1972b, 1974). It displays a constant configuration throughout the Therocephalia and is invariably present as a small, robust, dumbbell-shaped bone extending between the foramen ovale and the ventromedial surface of the quadrate. The lack of a stapedial foramen constitutes the main difference between the therocephalian stapes and that of other theriodont groups like the Gorgonopsia and the Cynodontia. The presence of a tympanum situated posteromedial to the quadrate has been accepted by virtually all previous authors except Allin (1975) and Kemp (1982). The latter author regards the stapes as too

bulky to have responded to high frequency air-borne sound and, in addition, pointed out that no obvious area for the attachment of a tympanum existed. In contrast Allin (1986), accepted the possibility of a tympanum located posteromedially to the quadrate in most therapsid taxa. This interpretation is further enhanced by the presence of a pronounced vertical sulcus on the posterior surface of the squamosal leading down to the alledged location of the tympanum in the nature of an external acoustic meatus as is seen in later cynodonts i.e. Diademodon.

The presence of stapedial processes has as yet not been satisfactorily demonstrated in the Therocephalia although reference has been made to a distally located dorsal elongation of the bone. Broom (1936c) described a dorsal process on the stapes of the advanced therocephalian Hofmeyria and mentioned a "well marked" process on the distal head in the holotype of the early therocephalian Lycedops scholtzi which, in his opinion, articulated with a cartilaginous extrastapedial. The occiput of Lycedops is weathered and has been somewhat crushed in an anterior direction. The distal head of the stapes abutts against the medial surface of the quadrate roller (Fig. 57e). From what is visible on the specimen it appears as if the quadrate roller is slightly imbedded in the head of the stapes. Broom (1936c) described the portion of the stapedial head lying above the roller as a dorsal process to which the extrastapedial attached. It appears however that this particular configuration of bone

should be interpreted as the result of a relatively slight amount of distortion rather than a distinctive morphological feature. Boonstra (1953c) described and figured a similar dorsal prolongation of the stapes in Therioides which he regarded as a base for the extrastapedial cartilage. Unfortunately the stapes is now lost in this specimen. According to Cys (1967) an early therocephalian identified by him as Cynariognathus also displays a dorsal elongation of the distal stapedial head. It is noteworthy that in this specimen the right temporal region of the skull appears to have been subjected to tangential stress and it is therefore possible that it may have affected the morphology of the stapes. In a later paper Cys (1971) mentioned the lack of a dorsal process in the advanced therocephalian Mirotenthes, where the distal head of the stapes firmly abuts against the inner face of the quadrate. From the description of Watson (1931) it appears that Ericiolacerta does not possess a dorsal stapedial process either. A dorsal process has however been recorded in cynodonts (Parrington 1946a, Fourie 1974) and gorgonopsians (Olson 1944, Kemp 1969).

Preparation of exsting as well as new material has supplied additional information. The skull of the scylacosaurid GS 273 (Fig. 13) is dorsoventrally crushed to the extent that the occiput lies in virtually the same plane as the palate. The distal head of the stapes abuts against the posteromedial portion of the quadrate ramus of the pterygoid and the medial surface of the quadrate roller. The

stapedial head is elongated and posteriorly projects towards the semicircular margin formed by the ventral and posteromedial borders of respectively the squamosal and quadrate, the location favoured by most previous authors as the site where the tympanum attached. Similarly, in Glanosuchus macrops GS RS962 the distal head of the stapes is posteriorly elongated to form a bony, process-like structure which extends towards the depression bounded by the margins of the squamosal and the quadrate (Fig. 20). This interpretation is further enhanced by the dorsoventral sulcus on the posterior surface of the squamosal leading to the alleged location of the tympanum in the nature of an external acoustic meatus as is also seen in later cynodonts i.e. Diademodon.

Kemp (1982) noted that in the Therocephalia the stapes does not abut directly against the quadrate. However, in the majority of the early Therocephalia it appears that the stapes does contact the quadrate. One exception seems to be Glanosuchus macrops GS RS962 (Fig.20), in which the distal head of the stapes fails to reach the quadrate. If this gap is real and not the result of damage, the possibility exists that a pad of cartilage may have separated the stapes and the quadrate. Such a pad would probably have facilitated stapedial movement.

The holotype of Lycosuchus vanderrieti (Figs 59b, 59e) in which a pronounced squamosal sulcus is present, the stapes is present as a thin, slightly displaced, dorsoventrally compressed element. The distal head, on which a small

posterior process is present, does not reach the quadrate and the gap may have been bridged by cartilage.

In Glanosuchus macrops GS M796, an unidentified stapes-like bone was discovered lying against the basisphenoid keel in close proximity to the actual position of the stapes. This small bone (Figs 14-19) does not readily resemble any other element in the skeleton. On what may be its posterior margin the remnant of a crest rather than a process is present. Despite the fact that its colouring and preservation almost certainly indicate that it forms part of GS M796, the identity of the bone remains uncertain because the fact that it was not attached to the skull indicates that it could have belonged to a different animal.

On the basis of the specimens discussed above it would be unwise to argue for the existence of a tympanum in the early Therocephalia. It may well be shown eventually that in cases where a stapedial process does exist it may not have had an acoustic function but instead supported the stapes against the paroccipital process as in the Pelycosauria. Additional investigation of this area is therefore required.

9. Lower jaw

The lower jaw of the early Therocephalia is quite distinct from that of the rest of the taxon, the most obvious differences being the robust aspect, the greater size and, in lateral view, the relatively straight ventral margin of the

dentary

The dentary (Figs 1,2,3,4,5,21,22,25) is a large, elongated element bearing a well developed complement of incisors and postcanines. A single, functional canine is always present. Anteriorly the dentary forms a loose symphysis with its opposite number. The symphysial surface is relatively smooth (Fig. 2), indicating a much looser contact than in either gorgonopsians or cynodonts. This feature is present throughout the Therocephalia and contrasts markedly with the condition in the Gorgonopsia where the symphysis is stronger and, especially the lower portion, more in the nature of an interdigitating suture (Fig. 31) The therocephalian mentum is also characteristic in that it is shallower and its anterior margin less steep than that of gorgonopsians. Consequently, in lateral view, the lower margin of the dentary gradually slopes in a posteroventral direction (Fig. 22). In contrast to other therocephalians i.e. Blattoidealestes (Boonstra 1954b), Theriognathus, Ictidosuchoides, Ictidosuchops (Brink 1982) the ventral margin of the bone is straight in lateral view (Fig. 22).

The anterior extremity of the dentary is medially and laterally swollen to accommodate the canine root and strengthen the symphysis. This has produced a shelf situated medial to the incisors and canine. A lesser shelf, through which replacement teeth erupt, lies directly medial to the postcanine tooth row. Immediately behind the canine position the lateral surface of the mandible is narrowed to accommodate

the crown of the upper fang when the jaw is adducted as in Figs 1 and 4.

A well developed anteroposteriorly directed gutter is present on the medial surface of the dentary (Figs 2,5). This structure is medially overlain by postdentary bones, primarily the splenial and the prearticular, to form the Meckelian canal. The posterior portion of the Meckelian canal forms a narrow gutter which terminates bluntly against the front end of the articular. The apparently rugose aspect of the articular at this point indicates that a portion of the meckelian cartilage persisted in this position in the early Therocephalia as it does in some recent vertebrates.

Posteromedially the dentary is broadly excavated to accomodate the anterior portions of the postdentary elements (Fig 25). At this point the ventral margin of the dentary curls inward to support these elements from below as well (Fig.21). In lateral view the posteroventral portion of the dentary forms a distinct angle (Figs 1,4,22). This contrasts with the condition found in the Gorgonopsia and the later Therocephalia where the ventral margin of the dentary exhibits a gradual upward slope without a distinct angle.

The outer surface of the mentum and anterior region of the dentary bear rugosities similar to those described on the snout. This condition is construed to indicate the absence of muscle attachment in this region (Figs 1,3,4,9).

Posterodorsally the prominent coronoid process extends into the anterolateral portion of the temporal fenestra. It

terminates well within the temporal vacuity and appears to have reached at least the level of the upper margin of the temporal arch. A sulcus is present on the ventral margin of the coronoid process.

According to Barghusen (1968) the Therocephalia resemble sphenacodont pelycosaurs e.g. Dimetrodon in that the adductor musculature did not extend laterally below the level of the zygomatic arch. In addition he (Barghusen 1968) points out that the space between the zygomatic arch and the lateral surface of the coronoid process is insufficient to have accommodated a substantial portion of the external adductor musculature. However, in undistorted specimens such as Lycosuchus vanderrieti US D173, even though the coronoid process is situated well laterally within the temporal vacuity, a relatively large gap is present between the zygomatic arch and the coronoid proc (Fig. 59a). In the same specimen a broad, shallow sulcus is present on the lateral surface of the coronoid process. This structure can also be observed in Lycosuchus keyseri GS C60 (Fig. 61a) and Glanosuchus macrops GS M796 (Fig. 50a). Because mammalian attributes such as a secondary palate and cusped teeth develope within the Therocephalia it is possible that the features mentioned above, viewed in conjunction with the lack of rugosities on the posterior portion of the dentary, probably indicate that a portion of the external adductor musculature or an extended aponeurosis might already have inserted on the lateral surface the coronoid process in the

early Therocephalia.

The splenial (Figs 2,21,25) extends anteroposteriorly along the medial surface of the dentary as a thin plate covering the meckelian canal. Anteriorly it enters the symphysis and posteriorly terminates at the level of the transverse process of the pterygoid, overlying the anterior portions of the prearticular and the angular. The particular nature of the splenial is distinctive throughout the Therocephalia in that it lacks the thickened anterior extremity of the Gorgonopsia. In ventral view the lower, inner margin of the jaw is therefore confluent with the symphysial line. Gorgonopsians on the other hand possess a splenial which is anteromedially thickened and the inner margin of the jaw executes a 90 degree turn towards the midline at the base of the mentum before it turns sharply forward into the symphysis (Fig. 31). In ventral view, therefore, the symphysial line of gorgonopsians and the lower margin of the dentary do not lie in the same plane. This feature is especially useful in the field to distinguish between weathered, terminal snout portions of therocephalians and gorgonopsians, which are very similar in other respects.

The coronoid (Figs 2,21,25) bone is a flat element situated against the base of the coronoid process of the dentary. An anterior process extends forward against the dentary for a short distance, directly above the anterodorsal margin of the prearticular. A ventral process medially overlies a portion of the prearticular whilst a dorsal process

medially overlies the contact between the coronoid process of the dentary and the surangular. The rear margin of the bone is concave, marking the posterior entrance to the covered portion of the meckelian canal.

The prearticular (Figs 1,21,23a,23b,25) forms an elongated strut against the medial surface of the rear half of the mandible. It is situated lateral to the meckelian canal but medial to the ventral process of the coronoid. Anteriorly it contacts the dentary and its ventral margin is overlain by the splenial. Posteriorly the bone deepens dorsoventrally, broadening the contact with the angular and meeting the articular in a strong contact which supports the latter anteromedially and ventromedially (Figs 23a,23b). In ventral view the prearticular covers the mandible posteromedially and contributes the medial portion of the posteroventral crest on the lower jaw (Fig 23b). Immediately anterior to the prearticular-articular contact a distinct anteroposteriorly elongated fossa is present on the dorsal surface of the prearticular. It is presumed that a portion of the pterygoideus musculature might have inserted here.

The surangular (Figs 1,2,4,5,21,22,23a,23b,24,25) is a strong, flat bone lying medially to and against the upper portion of the angular. Anteriorly it forms a thin prong, wedged between the coronoid, dentary, angular and prearticular (Fig. 25). The thickened, dorsal margin of the bone curves posteroventrally to meet the lateral portion of the articular dorsally, anteriorly and ventrally. Ventromedially the

surangular contributes to the posteroventral crest of the mandible. Anteromedially the lower margin of the bone is emarginated, exposing a portion of the medial surface of the angular and giving passage to the postdentary foramen. This aperture, situated between the angular and surangular, immediately behind the base of the coronoid process of the dentary, appears to be the precursor of the postdentary fenestra found in the later Therocephalia (Fig. 61e,61f). Posteromedially at the contact with the articular a small, deep fossa is present on the medial surface of the surangular.

The angular (Figs 1,2,4,5,21,22,23a,23b,25) is a thin, plate-like bone which forms the posterolateral portion of the mandible and covers most of the lateral surface of the surangular. Medially it forms the floor and lateral wall of the meckelian canal and is anteriorly clasped between the dentary, splenial and prearticular (Fig. 25).

Sphenacodont pelycosaurs, therapsids and Rhaetic mammals are unique amongst vertebrates in that the angular bone possesses a lateral outgrowth, the reflected lamina. This structure is well developed in the early Therocephalia and is present as a thin flange with freestanding posterior and ventral margins (Figs 1,4,5,21,25). The posterodorsal margin of the reflected lamina always bears a distinctive, anteroventrally orientated notch whilst the body of the lamina is strentghened by 5 ridges radiating from a point immediately anterior to the base of the notch. A dorsal ridge lies above the angular notch and a wide posterior ridge below the notch.

An anterior ridge extends horizontally forward with an anteroventral and a ventral ridge situated below the anterior ridge. Because of the configuration of the angular ridges a number of depressions are also present. A large depression is situated between the anterior and dorsal ridges whilst smaller depressions are present on each side of both ventral ridges (Fig.1).

The articular is a relatively small bone wedged between the posterior extremities of the prearticular and the surangular. Medially it is underlapped by the prearticular and laterally by the surangular. The glenoid is formed only by the articular and extends transversely and faces posterodorsally. In specimens where this region is complete it appears that the hinge-line at the temporo-mandibular joint extends posterolaterally. Immediately anterior to the glenoid a deep cone-shaped pit, which lacks a posterior wall, is present. The position of this structure is such that it probably served as a point of insertion for a portion of the pterygoideus musculature which pulled the posterior extremity of the jaw medially and anterodorsally.

Contrary to Boonstra (1953c) a retroarticular process is present (Fig. 24). Because of its exposed position on the skull this structure is always damaged and has therefore not been definitely identified in any of the known early Therocephalia. Nothing is known about its shape and size but the fairly stout base that is preserved in a single specimen i.e. Glanosuchus macrops GS M796, indicates that it was

probably a short, strong process.

10. Dentition

With the exception of the advanced whaitsiids, which lack postcanines, all members of the Therocephalia possess marginal incisors, canines and postcanines. Palatal teeth occur only on the pterygoid and, in contrast to the Gorgonopsia, the palatine is always devoid of teeth. Marginal precanines are infrequently present and a maximum of two may occur in the early Therocephalia, whereas up to three may be present in later therocephalians e.g. Tetracynodon darti (Sigogneau 1963).

The dentition of the early Therocephalia is simple and conical, with the marginal teeth somewhat compressed and recurved. The lower and upper tooth rows do not occlude as the former is positioned lingual to the latter when the jaw is adducted. A protective strip of keratinised integument, against which the lower postcanines bit, appears to have been present in the palate, medial to the upper postcanines. (See description of palatine)

In the Scylacosauridae the palatal teeth are predominantly grouped on the pterygoid boss but occasionally, what appear to be the roots of one or two small teeth, may be present on the proximal portion of the transverse process of the pterygoid e.g. Lycedops scholtzi (Fig. 57g). The Lycosuchidae possess teeth on the transverse process of the

pterygoid but never on the pterygoid boss. In the later Therocephalia it appears that when palatal teeth are present they are never located on the transverse process of the pterygoid but confined to the pterygoid boss as in the Scylacosauridae. According to Mendrez (1975) a small, badly preserved and very fragmentary specimen, BMNH R4096 Crapartinella croucheri, possesses an anteroposterior row of approximately 20 minute teeth on each vomer. These structures are difficult to evaluate and as they may be artefacts of preservation they are not here considered as teeth (own observation and Hopson pers. comm.).

Within the Therocephalia the most robust teeth are found amongst the Scylacosauridae and the Lycosuchidae. These two families are characterised by the possession of large canines and the presence of tooth serrations. The latter, present on both the anterior and posterior margins of all teeth, are aligned perpendicular to the long axis of each tooth (Fig. 33). Tooth serrations of this type are indicative of a carnivorous habit and are here regarded as a plesiomorphic feature, widespread amongst related and non-related taxa viz. sphenacodont pelycosaurs, gorgonopsians, cynodonts, dinosaurs, squamates and mammals. Tooth serrations are likewise also widespread amongst herbivorous taxa viz. squamates (Iguana), dinosaurs (Massospondylus), therapsids (Pristerodon) and cotylosaurs (Pareiasaurus). In these forms, however, the serrations are of the herbivorous type and quite unlike those found in carnivores.

The early Therocephalia possess from 5 to 7 upper incisors. In the Lycosuchidae the number is always 5, (but see Hyaenasuchus whaitsi SAM 1079), whilst among the scylacosaurids the number of upper premaxillary teeth may vary from 6 to 7. As this feature is constant within the early Therocephalia, the number of upper incisors is regarded as diagnostic. These teeth progressively increase in size from the first to the fourth and then decrease in size to the last tooth. The size of the incisors appears to be related to the height of the premaxilla at each tooth position, because the fourth tooth lies at the point where the bone is deepest and the hindmost incisor, which is the smallest, is situated where the bone offers the least amount of root space. Because of this it is difficult to obtain a clear picture of the mode of replacement amongst the upper incisors. However, as the canines and postcanines are replaced in alternate fashion it is likely that the incisors are too. Individually the incisors are replaced by a medial invasion of the alveolus. The tip of the replacement tooth erupts medial to the base of the functional incisor and migrates outwards, probably partially resorbing the root of the functional tooth at the gumline, as Van den Heever (1980) demonstrated for the canines.

There are always 3 lower incisors in the early Therocephalia as opposed to the rest of the taxon which possesses 4 lower incisors. According to Brink & Kitching (1953b), Brink (1963), and Brink (1982) Bauria possesses three lower incisors. However, the type of Bauria cynops SAM 1333

has 4 lower incisors in each dentary and according to Kitching (pers. comm.) the Bauria specimens held by the Bernard Price Institute all possess 4 lower incisors. Broom (1909b) recorded four lower incisors in Bauria as did Boonstra (1938). Both authors confirmed the lack of tooth serrations in this taxon.

An interesting aspect of the tooth serrations is the way in which they are orientated on the incisors. The anterior row of serrations on the first incisor face medially, whereas the rest are orientated in such a manner that an anteroposterior line drawn through the serrations on each tooth follow the curve of the premaxillary margin (Fig. 27).

Precanines appear not to occur in the Lycosuchidae but only in the Scylacosauridae and the later Therocephalia. Within the Scylacosauridae the number of precanines may vary from none to two. These teeth only occur in the maxilla, anterior to the forward canine position and are usually so small that they appear to be non-functional. It may be argued that the presence of precanines is indicative of an immature animal and that specimens like Scylacosaurus sclateri SAM 634, which possesses one precanine, are juveniles. That the specimen is mature, however, is shown by the way in which the sutures have knitted and by the robust aspect of the skull roof and postorbital arch. In addition, precanines are also present in large, undoubtedly mature specimens such as Therioides cyniscus SAM 11888. The presence of precanines is therefore considered a valid diagnostic feature and the number

of teeth is taken into account.

A large, functional upper canine is always present in the early Therocephalia. This tooth may be located in either one of two maxillary alveoli which alternately produce the functional canine and is contained in a prominent boss on the medial surface of the maxilla. For a discussion of the canine replacement sequence in the early Therocephalia see Van den Heever (1980). As the anterior canine alveolus is filled with progressively larger teeth after each replacement, the root of the anterior canine invades the alveolus of the posterior canine (Fig. 27, 63f). As the alveolus of the posterior canine enlarges through successive replacements, its root in turn invades the alveoli of the anterior postcanines as in Scymnosaurus ferox SAM 632 and Pristerognathus sp. SAM 9084a

As in mammals the large lower canine lies anterior to its upper counterpart when the jaw is adducted (Fig. 2). It erupts from a single alveolus of which the position is determined by the location of the internal choana in the palate. Because of its length the lower canine projects into the nasal cavity via the anterior portion of the internal choana. Since the position of the latter structure choana is fixed, it determines the single locality on the dentary from which successive replacements of the lower canine must erupt (Fig. 26). This means that the size of the crown of the lower canine will fluctuate from time to time.

The number of upper and lower postcanines differ in the early Therocephalia, the upper teeth always being fewer in

number. This condition is attributed to the presence of two canine alveoli in the maxilla and the fact that the development of the posterior canine alveolus erodes the anterior postcanine positions.

The maximum number of postcanines in both the maxilla and dentary appears to be 9. Mature lycosuchids with their relatively shorter snouts possess up to 5 upper postcanines, whereas the same teeth in mature scylacosaurids, with their longer snouts, number from 5 to 9. This condition appears constant and is here regarded as diagnostic. Previous taxonomic assessments have, however, utilised the exact number of upper postcanines to identify species. As the number of postcanine teeth is affected by the development of the posterior canine alveolus and it is not clear at present if new teeth are added at the back of the tooth row, the overall number of upper postcanines may actually decrease as the skull increases in size. The number of upper postcanine teeth has therefore no diagnostic value at specific level.

Romer & Price (1940) and Edmund (1960, 1962) have shown that in, respectively, pelycosaurs and most reptiles the teeth are replaced alternately by a succession of back to front waves passing through alternate tooth positions. In Ptomalestes avidus SAM 11942 and Lycosuchus keyseri GS C60 the lower postcanines appear to alternate in size indicating that replacement probably took place in alternate fashion as well. However, the overall size of the teeth decreases towards the back of the tooth row, suggesting that successive replacement

waves may have travelled from front to back in the early Therocephalia.

5. DESCRIPTION AND EVALUATION OF TYPE MATERIAL AND REFERRED SPECIMENS

Akidognathus parvus Haughton, 1918

Holotype

SAM 4021

Comments

This specimen was initially regarded by Haughton (1918) as closely allied to Scaloposaurus and Ictidognathus and placed in the Scaloposauridae, a view retained by Haughton (1924). Nopcsa (1928) placed the Scalopsauridae within the Suborder Gorgonopsoidea and divided the family into the Scalopsosaurinae and Akidnognathidae, the latter containing, amongst other taxa, Akidognathus. Broom (1932), on the other hand, grouped it with the early Therocephalia in a new family, the Ictidosauridae, containing Ictidosaurus, Scylacosaurus and Scylacorhinus. Camp and Vanderhoof (1940) recognised the Akidognathidae as a separate family. Romer (1945) transferred the specimen to the Alopecopsidae whilst Haughton and Brink (1955) referred the specimen back to the Akidnognathidae. Romer (1956) doubtfully placed it in the Pristerognathidae, whereas Watson and Romer (1956) grouped it with the advanced

Therocephalia as Bauriamorpha *incertae sedis*. Contrary to this view Romer (1966) yet again placed *Akidnognathus* as a doubtful pristerognathid.

The specimen is a fairly complete skull and lower jaw of a small therocephalian with portions of 4 vertebrae. The teeth are striated and lack serrations. These features definitely debar it from both the Scylacosauridae and the Lycosuchidae. The anterior portions of the vomers are also widened, a feature which indicates that the specimen is a member of the Akidnognathidae (=Euchambersiidae, Moschorhinidae, Annatherapsidae), a new grouping advocated by Hopson (1986).

Alopecideops gracilis Broom,1932

Holotype

SAM 4997 (not 4887 as in Broom, 1932 p. 66)

Material

Badly weathered and crushed skull and lower jaw of a small therocephalian.

Locality

Stinkfrontein, Prince Albert.

Collected

S. H. Haughton.

Original generic diagnosis

Skull probably measured 160 mm in greatest length and about 80 mm in breadth; interorbital measurement is about 20 mm; 6 incisors (20 mm); two small anterior canines and a moderately large third canine; 7 molars (25 mm) (after Broom 1932: 66).

Original specific diagnosis

As for genus.

References

Broom 1932: 66, Fig. 21c

Kuhn 1937a: 125

Romer 1945: 602

Haughton & Brink 1955: 127,138

Romer 1956: 697

Watson & Romer 1956: 69,87

Von Huene 1956: 317

Lehman 1961: 231

Vjuschkov 1964: 277

Kuhn 1965: 92

Boonstra 1969b: 53,61

Tatarinov 1974: 105

Kitching 1977: 44

Comments (Fig. 34 a-d)

Broom (1932) described and figured Alopecideops gracilis as a new genus and species allied to Pardosuchus whaitsi because both specimens appeared to possess two small canines anterior to a large third canine.

Alopecideops is crushed dorsoventrally to such an extent that in lateral view the postcanines in the right maxilla appear in cross section. The skull consists of three fragments, two of which comprise the postorbital portion, and the third the snout. There is no bony contact between the snout, which is slightly twisted in a clockwise direction, and the postorbital portion of the skull, but the fit appears quite close. The outer surface of the specimen is weathered away over the entire skull and lower jaw, leaving intact only two small areas of the original bone surface, one on the left maxilla and one at the mentum. The area around the external nares is weathered away, as is both the postorbital and temporal bars. On the left side the suspensorium is badly weathered.

The skull measures 147mm from the tip of the snout to the angle of the parietals but becuase of the distortion it is impossible to determine the exact overall length. Broom's (1932) measurement of 160mm is probably conservative.

The palate is partially exposed and shows a suborbital fenestra. It is not posible to determine with certainty if the frontals contribute to the dorsal borders of the orbits. A pineal foramen is present and the section through the

braincase shows a fairly narrow epipterygoid.

The tooth bearing areas on the specimen are severely damaged and no tooth shows serrations, striations or cusps. The number and the nature of the teeth are therefore not diagnostic.

On the right only a fragment of probably the first incisor is visible in the premaxilla. In the left premaxilla there are 5 incisors. The first is being replaced by an erupting tooth and has been partially resorbed. Between the fifth incisor and the functional canine is a large diastema. Broom (1932) described and figured two small canines in this region. Immediately anterior to the left canine is a single bone fragment which superficially resembles a tooth. If it is a tooth its position indicates that it would most likely be situated in the premaxilla and thus be an incisor. However, close examination of the inner aspect of the fragment indicates that it is confluent with the bone lying anterior to it and is therefore not interpreted as a small anterior canine but as the posterior extremity of the premaxilla.

The right premaxilla is badly weathered and only a fragment of the first incisor is preserved. There is no evidence of small anterior canines in the maxilla, but the roots of two large canines are present in the right maxilla, the anterior tooth being the largest. In the left maxilla a large canine is visible with an area of spongy bone behind it. This is usually found when a canine root is being resorbed. It appears therefore that the functional canine in this

specimen is the anterior one.

In the right maxilla there are 6 postcanines. Behind the fourth there is a diastema which may represent an additional tooth position but may also be the result of postmortem distortion since the left maxilla shows 6 closely packed postcanines.

Three incisors are visible in the right ramus of the lower jaw. However, the badly damaged root of a fourth tooth is visible immediately anterior to the canine (Fig. 34d). The possibility exists that this tooth may be a fourth incisor, in which case Alopecideops would definitely not be an early therocephalian. The preservation of the tooth is however too poor to substantiate this view and the tooth may equally well be a canine root. If it is a canine root it is probably the remainder of an earlier tooth and not that of a replacment canine since the latter usually develops medial to the functional canine.

Broom (1932) established the family Alopecodontidae for Alopecodon, Pardosuchus and Alopecideops, all forms which according to him possessed two small precanines in the maxilla. Other authors which followed Broom (1932) and included Alopecideops in the Alopecodontidae were Haughton and Brink (1955), Vjuschkov (1964), Boonstra (1969b) and Kitching (1977). Romer (1945) and Von Huene (1956) included Alopecideops in the Alopecopsidae whilst romer (1956), Watson and Romer (1956), Lehman (1961), and Kuhn (1965) placed the specimen in the Pristerognathidae. Tatarinov (1974) referred

Alopecideops to the Alopecodontinae as a subfamily of the Scylacosauridae.

Although Alopecideops gracilis superficially appears to differ substantially from the Scylacosauridae it seems even more remote from the non-scylacosaurid therocephalians of the Tapinocephalus-Zone like Crapartinella and Simorhinella. As a result of poor preservation the number and nature of the teeth are not diagnostic and there no other readily apparent features to diagnose this specimen conclusively. Because of the hardness of the matrix in relation to the bone and the poor condition of the specimen additional preparation may not be feasible.

Consequently, because the specimen is from the Tapinocephalus-Zone and possesses a long snout with more than 5 postcanines it is placed as Scylacosauridae incertae sedis.

Alopecodon priscus Broom, 1908

Holotype

SAM 920

Material

Anterior two thirds of a badly weathered, laterally compressed scylacosaurid skull and lower jaw.

Locality

About 14 kilometers N.W. of Seekoeigat, Prince Albert.

Collected

Presented by P.H. du Plessis.

Original generic diagnosis

Though allied to other previously known therocephalians, Alopecodon differs in having an unusually large number of incisor teeth (8); in front of the large canine is a small first canine as in Scylacosaurus; there were probably 8 molars (after Broom 1908a: 361-362).

Emended generic diagnosis

Alopecodon priscus has 7 incisors and 2 small canines in front of the large canine (after Broom 1925: 319).

Original specific diagnosis

As for genus.

Emended specific diagnosis

As for genus.

References

Broom 1908a: 361-363, Plate XLVI Fig. 2

Haughton 1924: 75,100

Broom 1925: 319

Broom 1932: 64-65, Fig. 21a

Boonstra 1934: 216

Boonstra 1935a: 2

Kuhn 1937a: 124

Haughton & Brink 1955: 139

Boonstra 1969b: 53,57

Kitching 1977: 43

Comments (Fig. 35a-c)

Broom (1908a) mentioned two skulls, fragmentary limbs, and vertebrae all found close together and in association with a large number of shells of the genus Palaeomutella. As he could not determine to which skull the postcranial material belonged, it was not included in the diagnosis. The skull which showed the teeth (SAM 920) was taken as the type of Alopecodon priscus and the second skull, presumably SAM 1209, was referred to the same taxon. No mention is, however, made in the South African Museum catalogue of postcranial elements associated with these two numbers, and only the two partial skulls are found in the collection.

Alopecodon priscus SAM 920 consists of the badly weathered anterior two thirds of a therocephalian skull. It has been laterally compressed and is fractured through the snout and lower jaw behind the ?fourth postcanine. It is an old weathered fracture and the two parts of the skull do not fit together. It has however been arbitrarily stuck together with plaster of Paris and consequently any estimate of the length of the snout can only be approximate.

Broom's (1908a) description is essentially correct, but his interpretation of the skull does seem to be at variance in

a number of points with what can actually be seen on the specimen.

The canines are not unusually long, as can be seen on the right side. The specimen has, however, been subjected to shear and the left side has been pushed down in relation to the right. It appears that the left canine has partially slipped from its alveolus and this gives the tooth the impression of being longer and more strongly curved than is usual. The canine measurements are therefore not diagnostic and contrary to the observations of Broom (1908a), serrations are present on the canines.

Anterior to each canine there are 9 teeth of varying sizes. Broom (1908a) believed the anterior 8 of these teeth to be incisors and the ninth tooth a very small canine. The right maxilla of Alopecodon priscus, which appears to have been less subjected to distortion than the left, shows a small diastema between the eighth and ninth precanine tooth. If this condition was visible in both maxillae it may have indicated the presence of eight incisors and one precanine. The preservation is however too poor to substantiate this interpretation. Behind each canine there is a large diastema indicating that the functional canine is situated in the anterior canine alveolus (see Van den Heever, 1980) and since replacement canines of the same tooth family develop medial to the functional canine none of the teeth anterior to the large canine is regarded as replacement canines. However, since no known scylacosaurid therocephalian has more than 7 incisors

and specimens are known that possess up to 2 precanines i.e. Pardosuchus whaitsi, the 9 teeth anterior to the functional canine in Alopecodon priscus is interpreted as 7 incisors and 2 precanines, the latter situated in the maxilla. This view agrees with that of Broom (1925, 1932).

The incisors vary in size. The first is very small, the second, third, and fourth larger and all about the same size, whilst from the fifth tooth they decrease rapidly in size to the very small number 7. Compared with other therocephalians the incisors of Alopecodon priscus seem unusually small but it may well be a growth phenomenon.

The postcanines are badly damaged, being sheared off laterally, resulting in Broom's (1908a) description of being flattened. On the left the remains of 4 crowns are visible, none with serrations. On the right 5 badly broken postcanines are seen of which only the second shows serrations along the posterior edge. Because of the complete break through the skull in the postcanine region it is impossible to determine the original number of postcanines. Broom (1908a) however, thought that the length of the maxilla and the size of the teeth indicated that the total number of postcanines were probably 8.

Broom's (1908a) description of the nasals appears to be correct but he noted that the external naris is supported inferiorly by a premaxillary process which passes between the maxilla and the nasal. The specimen is severely damaged in this area but it is obvious that he was in fact referring to

the septomaxilla. Because of damage to this portion of the skull the extent of the septomaxilla can only be guessed at but it appears to be no different to any of the other early Therocephalia.

The frontals are so weathered that they appear not to extend to the dorsal borders of the orbits and their anterior borders can also not be determined. Their sutures with the remnant of the postorbital and the parietal is however clear. Contrary to Broom's observations the frontals are not large, and their flat aspect is the result of weathering.

According to Broom (1908a) the temporal arch is formed by the jugal and the squamosal. This statement is true for therocephalians, but since the feature cannot be seen on the holotype of Alopecodon because it consists only of the anterior two thirds of the skull, he was probably referring to the second specimen, SAM 1209. However, since the type description is based on the teeth only, it cannot be stated with certainty that SAM 1209, which lacks the anterior half of the skull, belongs to the genus Alopecodon, and consequently the specimen cannot be employed to extend the description of the holotype.

In posterior view the epipterygoid is visible in section as a thin lamina of bone.

The dentary has the usual sloping mentum of the Therocephalia. Three incisors and a single canine are visible in each ramus of the lower jaw. The incisors decrease in size from the front to the back. Additional preparation has

revealed the existence of three postcanines, serrated both fore and aft, in each ramus of the lower jaw. The teeth are well spaced in the right ramus but seem to be dispositioned by distortion. Broom (1908a, Plate XLVI, Fig. 2) restored a large post-dentary foramen in the angular. This feature may have been present in life but cannot be seen on the specimen because it is too damaged.

Haughton (1924) placed Alopecodon in the Pristerognathidae whereas Williston (1925) and Nopcsa (1928) referred it to the Scylacosauridae. Broom (1932) placed it in a new family, the Alopecodontidae, together with Pardosuchus and Alopecideops. The Alopecodontidae was diagnosed as possessing two small canines anterior to a single large canine in each maxilla. Boonstra (1934) did not recognise the Alopecodontidae and regarded Alopecodon priscus as a pristerognathid. Both A. rugosus (Broom 1908a) and A. minor (Broom 1925) were referred by him to A. priscus. An additional specimen AMNH 5569 referred by Broom (1932) to A. minor was also placed as A. priscus by Boonstra (1935a).

From the above it is clear that the holotype of Alopecodon priscus SAM 920 is an extremely poor early therocephalian and, except for some features pertaining to the dentition, evinces an almost complete lack of diagnostic features. However, because it appears to possess 7 incisors and 2 precanines, a feature here regarded as diagnostic, the taxon is deemed valid.

Alopecodon priscus Broom, 1908

Referred specimen

SAM 921

Material

Preorbital portion of a small, badly weathered skull and lower jaw; lacking tip of snout, left ramus of lower jaw, as well as anterior half of right ramus.

Locality

Near Seekoeigat, Prince Albert.

Collected

Presented by P. H. du Plessis

Original generic diagnosis

Molars of the same flattened type as in *Alopecodon priscus*. Maxilla, mandible and other bones are of the same type as *A. priscus* (after Broom 1908a: 363).

Original specific diagnosis

Marked pitting on the surface of the upper part of the maxilla (after Broom 1908a:363)

References

Broom 1908a: 363-364

Haughton 1924: 75,101

Broom 1932: 65, Fig. 21E

Boonstra 1934: 216

Kuhn 1937a: 125

Haughton & Brink 1955: 139

Boonstra 1969b: 53

Comments (Fig. 36a-c)

Broom (1908a) described this specimen as Alopecodon rugosus, but expressed some doubt as to whether it belonged in the genus. However, because he regarded the postcanines, maxilla, mandible, and other bones to be similar to that of the holotype Alopecodon priscus, SAM 921 was retained in the genus Alopecodon. SAM 921 is so badly weathered that it is a particularly poor specimen. Moreover, Broom (1908a) did not include the specimen in the genus Alopecodon on the diagnostic features of the holotype, but on different features. He did not state, however, that the generic diagnosis was emended in any way. An additional problem is that the generic diagnosis given for SAM 921 is invalid since the so-called flattened postcanines of A. priscus are the result of weathering, and the similarity between the cranial elements of the holotype of Alopecodon priscus and SAM 921 is in reality no more than what would be expected to exist between any two members of the Therocephalia. The rugose surface of the left maxilla which, according to Broom (1908a) specifically isolates SAM 921 is

unfortunately a feature common to all early Therocephalia.

Contrary to the observations of Broom (1908a), but in agreement with Broom (1932), the remains of 7 postcanines can be seen in the left maxilla. In the right maxilla 6 postcanines are present. Because of the condition of the specimen this is by no means a final count and it can only be said that there were at least that number of teeth. A single canine is visible in the left maxilla. In the right maxilla two canines are present with the anterior tooth in the process of being replaced. The sulcus in the maxilla between the two canine alveoli (van den Heever 1980) can also be seen. The precanine region is not preserved in the specimen. In the lower jaw the roots of an indeterminate number of postcanines are visible in section.

Both the epipterygoid and the keel of the basisphenoid are only visible in section.

The postorbitals are distinct and the postfrontal also appears distinct. The frontals are slightly concave dorsally as is usual for scylacosaurids and in this respect differ from the description of the holotype of Alopecodon priscus in which specimen Broom (1908a) stated the frontals to be fairly flat. The dorsal surface of the frontals in the holotype has, however, been weathered off.

What little can be seen of the lower jaw shows that there is no special similarity in this region between the holotype of Alopecodon priscus and SAM 921.

Broom (1925) stated that SAM 921 probably did not belong

to the genus Alopecodon. Later (1932) he admitted that because the incisors were not preserved in the specimen he was unable to refer it to a specific genus. However, since SAM 921 was originally referred to Alopecodon by him, he retained it in that genus. Boonstra (1934) stated that because SAM 921 was so poorly preserved, and since he did not regard the smaller size of the specimen in relation to the holotype of Alopecodon priscus as diagnostic, he referred SAM 921, together with a second specimen, BMNH R5750, to Alopecodon priscus, a view retained by Haughton and Brink (1955), Boonstra (1969b) and Kitching (1977).

SAM 921 is an early therocephalian because the teeth show serrations, the presence of a postfrontal is indicated and the intertemporal region appears narrow.

Because the specimen lacks the anterior portion of the snout, the number of precanine teeth are indeterminate. Since Alopecodon priscus is based on the number of incisors and precanines it is therefore impossible to refer SAM 921 to this taxon. The generally poor state of the specimen and resulting lack of diagnostic features also preclude its placement in any other taxon. However, the presence of a large number of upper postcanines indicate that the specimen is not a lycosuchid. SAM 921 is therefore placed as Scylacosauridae incertae sedis.

Alopecodon priscus Broom, 1908

Referred specimen

AMNH 5569

Material

Extremely poor scylacosaurid snout fragment and partial lower jaw.

Locality

Fraserburg Road, Prince Albert

Collected

J.H. Whaits

References

Broom 1915a: 115

Broom 1932:65

Boonstra 1935a: 1-2

Kitching 1977:36

Comments (Fig. 37)

Broom (1915a) referred this fragment to Alopecodon priscus because he regarded it to have 8 incisors and 1 precanine but later, (Broom, 1932), placed it with Alopecodon minor because of its small size. At this point in time he regarded Alopecodon to possess 7 incisors and 2 precanines. Boonstra (1935a) doubtfully recognised all the teeth anterior to the large canine as incisors, and pointed out that because of the

differences in the numbers of teeth AMNH 5569 may belong to a different taxon. However, because the specimen was so poor, Boonstra (1935a) referred it to Alopecodon priscus.

AMNH 5569 is very fragmentary but it does have 3 lower incisors in the left dentary and is therefore an early therocephalian. The upper incisors are largely present as impressions and consequently no tooth serrations are visible. The suture between the premaxillae is indistinct but it appears that the left premaxilla possesses 7 incisors. In the right premaxilla there are apparently 6 teeth with a diastema between the second and fourth. The tooth fragment between the first and second tooth is probably that of a replacement. There are at least 6 postcanines in the right maxilla but because of a break through the snout in the postcanine region, the total number is indeterminate in both maxillae. The impressions of what appears to be 2 precanines in the right maxilla are present immediately anterior to the canine. No evidence of precanines is visible in the left maxilla.

AMNH 5569 is so poor that apart from the teeth no other diagnostic features are present. The specimen is, however, regarded to possess 7 incisors and 2 precanines and, in agreement with Broom (1932), is retained as Alopecodon priscus.

Alopecodon priscus Broom, 1908

Referred specimen

BMNH R5750

Material

Badly weathered snout of a scylacosaurid therocephalian with anterior third of lower jaw.

Locality

Abrahamskraal, Prince Albert.

Collected

Unknown (purchased from R. Broom)

Original generic diagnosis

See holotype of *Alopecodon priscus* for generic diagnosis of *Alopecodon*.

Original specific diagnosis

The canine in *Alopecodon priscus* is much flattened, here it is broadly oval in section; there are 7 molars and quite possibly the first preserved molar is the second. (after Broom 1925: 319-320).

References

Broom 1925: 319-320

Broom 1932: 65, Fig. 21b

Boonstra 1934: 216

Kuhn 1937a: 125

Haughton & Brink 1955: 139

Boonstra 1969b: 53

Kitching 1977: 32

Comments (Fig. 38)

Broom (1925) described this specimen as a new species, Alopecodon minor, but it was never figured. In the same article he changed his view that the holotype of Alopecodon priscus (Broom 1908a) possessed 8 incisors and one precanine, to state that it possessed 7 incisors and 2 precanines as in Alopecodon minor, a view retained by Broom (1932). The species A. minor was therefore based on the fact that it presumbaly had one postcanine less, and a less flattened canine than the holotype of A. priscus. Later, Broom (1932: 65) regarded both A. priscus and A. minor to possess 8 postcanines and, in addition, referred the specimen AMNH 5569 to the latter taxon. The only difference then left between Alopecodon priscus and Alopecodon minor was the smaller size of the latter and the 'broadly oval' appearance of its canine in section. However, an oblique section through the base of the canine crown as in BMNH R5750 appears oval in any scylacosaurid and is not diagnostic at specific level. Boonstra (1934) also correctly pointed out that a difference

in size such as that between A. priscus and A. minor was insufficient to distinguish taxa on.

According to Boonstra (1934) BMNH R5750 has 6 closely packed postcanines followed by an empty socket, medial to which lies a small tooth. On the specimen it is clear however that there are at least 7 postcanines in the right maxilla and what may be a small additional alveolus is present behind the last tooth.

Boonstra (1934) stated that he could find no evidence that the last two teeth anterior to the canine are implanted in the maxilla and that they may well be incisors. A large diastema is present in the right maxilla behind the canine indicating that the fang is situated in the anterior canine alveolus. The teeth anterior to the canine are therefore either precanines or incisors. However, the suture between the two premaxillae is indistinct and the correct number of incisors cannot be determined. It is possible though that there may be 7 incisors and 2 precanines.

The mentum is that of an early therocephalian, but no serrations are visible on any of the teeth. The lack of tooth serrations are almost certianly the reuslt of the poor preservation and they may well have been present in life.

Boonstra (1934) referred both Alopecodon minor and Alopecodon rugosus to A. priscus, a view shared by Haughton & Brink (1955) and which was retained by Boonstra (1969b). The specimen is, however, so fragmentary that the only possible diagnostic feature is the number of teeth. Since the exact

number of incisors is indeterminate and the number of precanines are also in doubt, it is not possible to confidently refer this specimen to any one taxon. BMNH R5750 is therefore not regarded as a referred specimen of Alopecodon priscus but placed as Scylacosauridae incertae sedis.

Alopecognathus angusticeps Broom, 1915

Holotype

AMNH 5559

Material

Badly weathered and laterally crushed scylacosaurid skull and lower jaw, lacking right postorbital and temporal arches, and dorsal portions of parietals and squamosals.

Locality

Grootfontein, Beaufort West.

Collected

J. H. Whaits

Original generic diagnosis

Large therocephalian from upper Pareiasaurus zone; skull narrow and deep; orbits near middle and relatively small; frontal region unusually small; parietal region forms narrow

crest; distance from orbit to front of snout 143mm; greatest length of skull 276mm; greatest width probably 140mm; 6 incisors with posterior one much flattened; most incisors, probably all, serrate behind; incisors occupy space of 33mm; between sixth incisor and canine there is an unusually short diastema (7mm); canine relatively small and slender (width 12mm, length 30mm); probable first molar situated 15mm behind canine and whole series of 6 molars occupy space of 33mm; angular large oval bone, somewhat corrugated but lacks peculiar cross bar of gorgonopsians. (After Broom, 1915a: 116).

Emended generic diagnosis

Moderate to fairly large pristerognathids with dental formula I.6, C.1, Pc.4-5; anterior incisors fairly long, slender teeth (first, as in all pristerognathids, smaller than second to fifth but sixth appreciably to very much smaller); canine long and strong; postcanines small and fairly weak, not close set; skull moderate to fairly large (maximum length 240?-276mm); preorbital hollow varies from a fairly shallow hollow shallowing evenly in the direction of the canines and without abrupt borders to a deep depression with sharply demarcated borders especially anteriorly; septomaxilla with well developed facial exposure and septomaxillary foramen well developed; frontal with small entry into orbital border or just excluded from it; prefrontal large with well marked dorsal and lateral face; postfrontal moderately to well developed; snout wider than high, broader over last

postcanines than over canines; orbits just entering anterior half of skull; mandibular symphysis weak and mentum sloping very much; sagittal crest of parietals moderately high but with sharp edge; quadrate low down, but well above the level of the lower border of the dentary; temporal fossa fairly long and wide; squamosal with everted lateral edge (after Boonstra 1954a: 88).

Original specific diagnosis

As for genus.

Emended specific diagnosis

There are 5-6 postcanines; maximum length of skull 275 mm; preorbital depression fairly shallow to deep, extending in the direction of the canine; postfrontal well developed; squamosal laterally everted (after Boonstra 1954a: 88).

References

Broom 1915a: 116, Fig. 6

Haughton 1924: 75, 101

Broom 1932: 56-57, Fig. 17D.

Boonstra 1935a: 2-5, Figs 1-2

Broili & Schröder 1936a: 12,13

Kuhn 1937a: 120

Romer 1945: 602

Boonstra 1954a: 88,92

Haughton & Brink 1955: 128

Kuhn 1965: 93

Kitching 1977: 36

Comments (Fig. 39a-c)

Alopecognathus angusticeps AMNH 5559 is a fairly complete skull, but weathered over its entire surface. It is laterally compressed to the extent that the left postorbital arch is directed posterolaterally. Because of this the left orbit is enlarged and has an oval appearance. The dorsal border of the angular is turned outward and it appears to be the result of being dorsally compressed against the ventral surface of the coronoid process. The outer surface of the skull has been previously subjected to extensive grinding and this process effectively destroyed the outer layer of bone.

Broom (1915a) established Alopecognathus angusticeps on generalised scylacosaurid features. He recorded the dental formula as I.6,C.1,Pc.6 in the text but in the accompanying figure as I.5,C.1,Pc.7. Later, (Broom, 1932) he emended the dental formula to I.6,C.1,Pc.8 and stated that A. angusticeps was a near ally of Pristerognathus vanderbyli, but differed in possessing two additional molars, a skull which was much deeper behind, and a differently shaped jugal and dentary. Broom (1932) also mentioned the possibility that Pristerognathus polyodon and Pristerognathus baini belonged to the genus Alopecognathus. However, owing to the poor state of these types, the question could not then be resolved. From Broom's (1932) illustrations (Figs 17A&D) the differences

between Pristerognathus vanderbyli and Alopecognathus angusticeps are not clear at all but the similarity seems apparent. Boonstra (1935a) described and illustrated the skull after additional preparation. He found a replacing tooth behind the second postcanine and gave the dental formula as I.6/I.?, C.1/C.?, Pc.5/Pc.?

The specimen has 6 serrated incisors in each premaxilla. The posterior incisors are not 'much flattened' as according to Broom (1915a) but similar to the incisors of other scylacosaurids. Broom (1915a) noted the 'unusually short diastema' (7mm.) between the sixth incisor and the canine. This feature is present on the right side only, since the diastema on the left side is almost double that (13mm). A single large serrated canine is present. In the left maxilla the remains of 5 well spaced postcanines are seen. In the right maxilla 4 postcanines are present with a space between the first and second tooth and a large space between the third and fourth tooth. The second and third tooth lie close to one another. The small replacement tooth in the left maxilla behind the second postcanine indicates that additional postcanines may have been present in the spaces between the existing postcanines. It is therefore not possible to correctly determine the original number of postcanines in this specimen.

Unable to expose the occiput and the palate, Boonstra (1935a) only described the dorsal and lateral surfaces of the skull. He interpreted the skull as long and narrow, and his

description is that of a generalised scylacosaurid. Because of this he regarded A. angusticeps as closely related to other generalised scylacosaurids such as Scymnosaurus and Pristeroganthus.

Boonstra (1935a) illustrated the posterolateral borders of the squamosals as laterally everted. He did not, however, mention it in the text or regard it as diagnostic. Later, (Boonstra, 1954a) he believed this feature to be important enough to include in the diagnosis of the genotype for the taxon. His referred specimen, SAM 9112, from Stinkfontein, Prince Albert, does not have the relevant skull portion present and the feature is also not present in the type of Alopecognathus angustioriceps SAM 9342. The so-called laterally everted squamosal is only present in Alopecognathus angusticeps AMNH 5559 and is clearly an artefact of distortion.

It should be noted that both Broom (1932) and Boonstra (1935a) agreed on the difficulty of determining sutures on this specimen. Boonstra (1935a) stated that the postfrontal could only be a small element, but later, (1954a), described the postfrontal as well developed and included this feature, albeit common to all early Therocephalia, as part of the specific diagnosis of A. angusticeps. Broom (1915a) described the canine as relatively small and slender. Boonstra (1935a) interpreted it as medium sized, whilst Boonstra (1954a) regarded it as long and strong. According to Boonstra (1954a, p.88) the genotype of Alopecognathus has 4-5 postcanines but

in the specific diagnosis of A. angusticeps, based on the same specimen, it is said to have 5-6 postcanines. A shallow preorbital depresssion is present. On the left there is, contrary to Boonstra (1954a), no anterior extension in the direction of the canine. On the right, as a result of distortion, a broad depression extends anteroventrally in the direction of the anterior postcanines. The remaining features comprising the specific diagnosis of A. angusticeps are a repetition of those included in the generic diagnosis of the taxon.

It appears therefore that because the skull is not fully prepared, and owing to the intractable matrix it may never be, the features utilized in the diagnoses are those expected to be present in a generalised early therocephalian, and not necessarily diagnostic of any specific taxon. It does appear, however, that AMNH 5559 should resort with the more slender skulled taxa.

It should be noted that Boonstra (1969b) diagnosed the genus Alopecognathus as moderate to fairly large Pristerognathinae with an upper dental formula of I.6,C.1,Pc.4-6, and laterally everted squamosals. Of the 4 species mentioned by him, Alopecognathus skinneri is an error because the only early therocephalian ever to have had the specific name of skinneri, is Karroowalteria skinneri, a taxon which Boonstra (1969b), in the same article, synonymized with Pristerognathoides. Of the remaining 3 species, A. megalops does not conform to the diagnosis of the genus, a fact

previously noted by Haughton and Brink (1955). The remaining taxon, A. angustioriceps, can also not be included in the genus Alopecognathus on the basis of the listed features because the diagnosis is too vague.

Therefore, since the single unique feature in AMNH 5559, i.e. the laterally everted squamosal, is an artefact, and the rest of the diagnosis of the taxon is based on generalised early therocephalian features, Alopecognathus angusticeps is a nomen dubium. However, because the specimen has a slender skull, a relatively long snout, 6 incisors, and no precanines, it is here referred to Glanosuchus macrops.

Alopecognathus angusticeps Broom, 1915

Referred specimen

SAM 9112

Material

Badly weathered and crushed skull of a scylacosaurid therocephalian lacking the occiput, skull base, posterior portions of both lower jaw rami, dorsal portion of snout and right maxilla; lateral portion of right jaw ramus badly damaged; with ten bone fragments, mostly postcranial.

Locality

Stinkfontein, Prince Albert

Collected

L.D. Boonstra

References

Boonstra 1954a: 88-89, 92, Fig. 9

Kitching 1977: 44

Comments

A very poor specimen with 5 incisors and a diastema in the first icisor position for an additional tooth. The left preorbital depression is deep but has been ground out mechanically and, whilst the right preorbital depression appears very shallow, it must be pointed out that the whole postcanine portion of the skull has been badly weathered. On account of this specimen Boonstra (1954a) noted that the sagittal crest of Alopecognathus angusticeps AMNH 5559, as described by him in 1935, should actually be higher. The portion on the referred specimen which indicates that a sagittal crest was present is, however, glued to a second portion which in turn contacts the preorbital portion of the skull, and in view of the distortion present in the skull, does not afford conclusive evidence for a sagittal crest as high as in Boonstra's (1954a, Fig. 9b) illustration. Contrary also to Boonstra (1954a), the frontal suture is not preserved in SAM 9112 because of extnesive weathering and consequently cannot influence the interpretation of the same suture in the

genotype.

Because no other diagnostic features are apparent on the skull, the specimen is referred to Glanosuchus macrops because it possesses 6 incisors and lacks precanines.

Alopecognathus angustioriceps Boonstra, 1953

Holotype

SAM 9342

Material

A badly weathered and laterally compressed scylacosaurid skull lacking most of the outer surface of the snout, the left postorbital arch, the left temporal arch, and the left postdentary bones.

Locality

Kroonplaas or Heuningskopfontein, Beaufort West.

Collected

L. D. Boonstra

Original generic diagnosis

See holotype of Alopecognathus angusticeps for generic diagnosis.

Original specific diagnosis

'It differs from the genotype in its smaller size (252mm) and in having a more slender skull' (Boonstra 1953c: 63).

Emended specific diagnosis

'There are 5 postcanines; maximum length of skull 252mm; preorbital depression shallow, continued anteriorly as a shallow groove; postfrontal small; squamosal with lateral bulge' (Boonstra 1954a: 90).

References

Boonstra 1953c: 63 Fig. IVd

Boonstra 1954a: 89-92 Fig. 10

Haughton & Brink 1955: 128

Lehman 1961: Fig. 2

Kuhn 1965: 93

Boonstra 1969b: 57

Kitching 1977: 39

Comments (Fig. 40 a-d)

Alopecognathus angustioriceps has been crushed laterally giving the apparently slender skull an even more elongated appearance. In the process the squamosals and posterior portions of the parietals were pushed inwards and backwards. As a result of this the temporal fenestrae have been lengthened in an anterosposterior direction and the posteromedial angle between the parietals narrowed. The dorsolateral portion of the right squamosal is missing and the

middle portion of the right temporal arch has been displaced medially.

The specimen has also been previously treated in acid and, with regard to the occiput and jaw articulation, the sutures cannot be determined with any certainty. Boonstra, (1953c) in his description of the relationship between the quadrate and the quadratojugal correctly pointed out that the quadratojugal did not form part of the jaw articulation. Because of the relationships of the distal portion of the paroccipital, the concave ventral edge of the squamosal and the internal corner of the quadrate condyle, Boonstra (1953c) regarded this area to be the locality of the tympanic membrane. He also noted that there was no notch in the reflected lamina of the angular. The ventral portion of the postdentary bones anterior to the articulation are, however, missing, together with most of the reflected lamina of the angular, which is the real reason why the angular notch is not visible. What can be seen on the angular, however, is that the dorsal margin of the bone, directly behind the angle of the dentary, is gently emarginated to form a postdentary foramen.

Boonstra (1954a) emended the specific diagnosis of Alopecognathus angustioriceps as given by him in 1953. There are indeed at least 5 postcanines in the right maxilla. In the left maxilla at least 4 postcanines are present but the specimen is so badly weathered that any postcanine count would not necessarily be correct.

In the right premaxilla 6 serrated incisors are present of which the fourth appears to be the largest, as is usual in early therocephalians. Anterior to the large canine on the left the suture between the maxilla and premaxilla is visible.

A single large canine is present in the anterior alveolus of both maxillae. Because of the severe weathering of the external surface of especially, the snout, an earlier, smaller canine has been laterally exposed in the posterior alveolus of the left maxilla. The tooth is visible as a root only and the dorsal portion is still intact. The ventral portion is cancellous and is in the process of being resorbed from the gumline upwards.

Boonstra (1953c, 1954a) based the overall skull length on the distance from the snout to the posterior edge of the squamosals. Since the squamosals have been distorted in a posterior direction, this measurement is enhanced. The distance from the snout to the occipital condyle is 220mm and a more realistic skull length would therefore be 230mm. The presence of a shallow preorbital depression and its associated groove is not diagnostic at specific level for members of the early Therocephalia.

The interorbital region of the skull is so badly damaged that an objective appraisal of the constituent bones cannot be made. According to Boonstra (1954a) the squamosal has a lateral bulge. The temporal region of A. angustioriceps is badly crushed inwards but the articulatory region has not been displaced medially as far as portions of the squamosal because

of the resistance of skull base and the paroccipital process of the opisthotic to medial crushing. Dorsal to this area the squamosal has been displaced medially and posteriorly, and anterior to the articulation the angular, surangular and the dorsal portions of the coronoid process have also been displaced medially. The unique shape of the squamosal in A. angustioriceps is therefore an artefact of distortion and consequently not diagnostic.

The parabasisphenoid and pterygoid form a well developed ventromedian keel behind the interpterygoid vacuity. The transverse processes of the pterygoids are damaged but appear to have been toothless. Medial to each suborbital fenestra lies a pterygoid boss which bears teeth. The boss on the right bears at least 14 small teeth and each boss extends slightly anterolaterally as a pterygopalatine ridge.

An unusual feature of the specimen is that between the two pterygoid bosses, immediately anterior to the interpterygoid vacuity, a small, distinct ventromedian crest (Fig 40d) is present on the palate, similar to that found in advanced Therocephalia, the holotype of Glanosuchus macrops SAM 637 and the holotype of Pristerognathoides vanderbyli MM 5139. From the height of the parietals behind the parietal foramen it appears that a sagittal crest was present.

Neither of the existing specific diagnoses for this specimen (Boonstra 1953c: 63, Boonstra 1954a: 90) is diagnostic and therefore become invalid. However, because the specimen possesses 6 upper incisors, a ventromedian crest on

the pterygoid and lacks precanines it is here referred to Glanosuchus macrops.

Alopecognathus megalops Broom, 1937

Holotype

TM 1491

Material

Weathered scylacosaurid skull lacking the occiput, anterior part of the snout and lower jaw, left postdentary bones, right temporal arch, dorsal portion of the right coronoid process and left squamosal.

Locality

Abrahamskraal, Prince Albert.

Collected

W. van der Byl

Original generic diagnosis

See holotype of *Alopecognathus angusticeps* for generic diagnosis.

Original specific diagnosis

In general structure the skull agrees pretty closely with *Pristerognathus minor* (Haughton). The new skull differs from *Pristerognathus* in having eight molars (after Broom 1937a:

141).

References

Broom 1937a: 141, Figs 1,2

Haughton & Brink 1955: 128

Kuhn 1965: 93

Boonstra 1969b: 57

Kitching 1977: 32

Comments (Fig. 41a-c)

This specimen is crushed dorsoventrally and dorsal surface of the skull is heavily weathered anterior to the pineal foramen but the frontals can be seen to extend to the dorsal borders of the orbits. The suture with the prefrontal is clear.

The number of incisors are indeterminate and the anterior part of the lower jaw is missing, as are the lower incisors and canines. Four lower postcanines are visible of which the most complete one is serrated both in front and behind. In the left maxilla 8 postcanine roots are visible as noted by Broom (1937a). This specimen is smaller than Pristerognathoides (Alopecognathus) minor and the large number of postcanines may indicate that the canine replacement cycle had not yet produced fangs in the posterior alveolus large enough to resorb the anteriormost postcanine alveoli. Broom's (1937a) measurement of 210mm for the skull length is too ambitious and it was in all probability not more than 190mm.

His other measurements (skull width 112mm and interorbital width 35mm) are correct. Both the parietal foramen and the condition of the postfrontal are usual for scylacosaurids.

The palate has been so damaged by previous preparation that no surface detail can be determined with certainty. On both sides, however, a pterygoid boss is present on the palate immediately anterior to the proximal portion of the transverse process of the pterygoid. What appears to be the root of a single tooth is situated in the left pterygoid boss. Indistinct structures resembling the roots of perhaps 4 teeth are also visible on the proximal portion of the transverse process of each pterygoid.

A parabasisphenoid keel is present and the dentary has a well developed angle. The condition of the lacrimal cannot be determined but the left postorbital lies in the correct position and forms part of the postorbital arch. The anterior extremity of the frontal extends to a point in line with the anterior border of the orbit but appears to be broken and may have been longer.

The ventral border of the lower jaw is weathered but appears to have been straight in contrast to the dorsal border which executes a gentle upward curve towards the tip of the coronoid process. The right dentary has a shallow sulcus on its lateral surface extending towards the coronoid process as in Lycosuchus vanderrieti US D173. In Fig. 41b this structure is slightly enhanced because of the stereo effect.

Haughton and Brink (1955) remarked upon the dental

formula of this specimen and pointed out that it differed from that given by Boonstra (1935a) for the genotype A. angusticeps AMNH 5559 which according to him possessed only 5 upper postcanines but a similar number of incisors and canines. According to Haughton and Brink (1955) A. megalops may, because of this condition, belong to a different genus. Boonstra (1969b) retained A. megalops in the genus and stated (p. 52) that the dental formula for the upper teeth in this genus was I.6, C.1, Pc. 4-6.

Since the number of incisors are indeterminate and the specimen evinces no other diagnostic features Alopecognathus megalops is here regarded as a nomen dubium. However, since it appears to have possessed a large number of postcanines it may be grouped as Scylacosauridae incertae sedis.

Alopecorhinus parvidens Broom, 1912

Holotype

AMNH 5503

Material

Badly weathered therocephalian skull fragment with portions of the premaxillae, maxillae, vomers and both lower jaw rami.

Locality

Beaufort West Commonage.

Collected

J.H. Whaits.

Original generic diagnosis

Differs from Pristerognathus platyrhinus in having a much more slender jaw and in the relatively smaller size of the teeth, especially the molars, and in having a much shorter precanine portion of the snout; at least 7 small, pointed, and apparently unserrated upper molars present; 4 lower incisors present, the fourth inside the line of the others; canine far forward, small and rounded in section (after Broom 1912: 864-865).

Original specific diagnosis

As for genus

References

Broom 1912: 864-865, pl. XCI 9

Haughton 1924: 76,101

Broom 1932: 57, Fig. 18E, F

Boonstra 1935a: 5

Kuhn 1937a: 122

Romer 1945: 602

Haughton & Brink 1955: 128

Romer 1956: 697

Von Huene 1956: 316

Watson & Romer 1956: 69,87

Lehman 1961: 231

Vjuschkov 1964: 276

Kuhn 1965: 93

Kitching 1977: 48

Comments (Fig. 42a-b)

The specimen is a therocephalian because it has a sloping mentum and the ventromedial border of the lower jaw forms a continuous line with the symphysis. Both Broom (1912) and Boonstra (1935a) noted that the specimen possesses 4 lower incisors. This feature alone shows that it is not an early therocephalian and, since it is from the Cistecephalus-Zone (Kitching 1977), it is in all likelihood a later therocephalian. Unfortunately it is so badly damaged that the number of upper incisors are indeterminate. Broom (1912) and Boonstra (1935a) agreed that the probable number was 6. However, if the specimen is a later therocephalian, which appears certain, it would have possessed no more than 5 upper incisors. Broom (1912) was also of the opinion that the teeth were probably unserrated. Since the teeth are present as roots only, this statement cannot be verified.

Unfortunately all authors subsequent to Broom (1912) have regarded the specimen as a pristerognathid. Even Boonstra (1935a p. 5) who remarked upon it as 'simply another name which encumbers scientific literature, without adding to our

knowledge of the Therocephalia', grouped it with the Pristerognathidae, as did Kitching (1977) who correctly regarded Alopecorhinus parvidens as a nomen dubium.

Arctosuchus tigrinus (Owen), 1876

Holotype

BMNH R1719

Comments

Preorbital portion of gorgonopsian skull regarded by Broom (1932) as an early therocephalian. Sigogneau (1970) placed it as Theriodontia incertae sedis.

Arnognathus parvidens Broom, 1907

Holotype

SAM 1069

Material

Right dentary of a scylacosaurid therocephalian lacking distal portion of coronoid process and portion of angle.

Locality

Victoria West. (See comments)

Collected

T. J. R. Scholtz.

Original generic diagnosis

It resembles the jaw of Ictidosuchus primaevus in being long and slender, in having a series of small pointed molars and having apparently no incisors. It differs in having the angle much more marked and in having the end of the jaw dilated (after Broom 1907a: 38).

Original specific diagnosis

As for genus.

References

Broom 1907a: 38-39, Fig. 6

Haughton 1924: 75

Broom 1932: 78,81, Fig 27G

Romer 1945: 602

Haughton and Brink 1955: 140

Von Huene 1956: 321

Romer 1956: 699

Watson and Romer 1956: 86

Romer 1966: 373

Kitching 1977: 69

Comments (Fig. 43)

Ever since Arnognathus parvidens was established by Broom (1907a), it has been accepted as an advanced therocephalian. Broom (1907a) himself regarded it as allied to Ictidosuchus primaevus and Theriodesmus phylarchus. Haughton (1924), Haughton and Brink (1955) and Von Huene (1956) all placed the specimen within the Ictidosuchidae. Broom (1932) grouped it with the later, non-pristerognathid therocephalians. Romer (1945) doubtfully referred it to the Scaloposauridae whilst Romer (1956, 1966) regarded it as a probable member of the Lycideopsidae. Watson and Romer (1956) grouped it as Therapsida incertae sedis. Kitching (1977) placed the specimen as Therocephalia incertae sedis and although he regarded the locality as within the Cistecephalus Zone, he did point out that it was unreliable. According to Keyser and Smith (1979) the locality falls within the confines of the Tapinocephalus Zone (Dinocephalian and Pristerognathus/Diictodon Assemblage Zone).

The specimen has a sloping mentum and the symphysis is confluent with the ventral margin of the dentary, definitely indicating that it is a therocephalian. The incisors and canine have been lost but the presence of a posteroventral angle on the dentary and, contrary to the observations of Broom (1907a), serrations on the postcanine teeth show conclusively that it is an early therocephalian. The lateral surface of the coronoid process shows a long anteroposterior depression which presumably facilitated the insertion of portions of the external adductor musculature. Because of the

latge number of postcanines (probably 10) the specimen is not a lycosuchid. However, since additional diagnostic features are lacking, Arnognathus parvidens is here regarded as a nomen dubium and placed as Scylacosauridae incertae sedis

Broomisaurus planiceps Broom, 1913

Holotype

AMNH 3752

Comments

Snout described by Broom (1913c) as Scymnorhinus planiceps and provisionally placed in the Therocephalia. Joleaud (1920) referred it to he genus Broomisaurus because Scymnorhinus was preoccupied. Haughton (1925) placed the specimen in the Pristerognathidae but Broom (1932) correctly described and figured it as a gorgonopsian, a view shared by all subsequent authors, noteably Sigogneau (1970) in her systematic revision of the South African Gorgonopsia.

Cerdodon tenuidens Broom, 1915

Holotype

BMNH 49420.

Material

Crushed and imperfect partial skull of a small early therocephalian.

Locality

Koup, Beaufort West

Collected

T. Bain.

Original Generic diagnosis

Probably five upper incisors; those remaining are slender and pointed; canine relatively small (4,5 by about 12mm); possibly seven or eight molars; lower jaw slender with low symphysis; appear to be three lower incisors; lower canine unusually small (after Broom 1915b: 166-167).

Original specific diagnosis

As for genus

References

Broom 1915b: 166-167, Fig 3

Haughton 1924: 75,100

Broom 1932: 81, Fig 26D

Boonstra 1934: 232

Romer 1945: 602

Haughton & Brink 1955: 129

Romer 1956: 688

Von Huene 1956: 321

Watson and Romer 1956: 55,87

Vjuschkov 1964: 262

Kuhn 1965: 24

Kitching 1977: 36

Comments (Fig. 44)

According to Broom (1915b) the snout of the specimen is too damaged to accurately determine the number of upper incisors but he judged there to be 5. He regarded the dentary to have 3 incisors. The anteriormost lower incisor that was present, was taken to be the first tooth in the other jaw ramus. He also stated that Ictidosuchus primaevus was closely related to Cerdodon tenuidens and included both specimens in the therocephalian family Ictidosuchidae. Haughton (1924) included Cerdodon tenuidens in the Ictidosuchidae together with Arnognathus and Ictidosuchus.

Broom (1932) maintained this view but increased the number of incisors to 6, reduced the number of postcanines from 'probably 7 or 8' to 5 and stated that the dentary has 4 incisors, 1 canine and 5 postcanines, as opposed to his previous view (Broom 1915b) of 3 incisors, 1 canine and 3 postcanines.

Boonstra (1934) found serrations on the crowns of the lower postcanines and gave the tooth formula as I.4/I.3, C.1/C.1, Pc.4/Pc.3. In addition Boonstra (1934) had sections cut from the specimen. This exercise proved unsuccessful and

nothing further could be determined about the specimen.

The presence of serrated teeth precludes the specimen from being anything but an early therocephalian or a gorgonopsian. However, the premaxilla and dentary is so incomplete that the exact number of upper and lower incisors and postcanines cannot be determined. No gorgonopsian or scylacosaurid is known to have only four upper incisors and in view of the different number of teeth proposed by Broom (1915b, 1932) and Boonstra (1934) it is advisable to regard the number of upper incisors as indeterminate.

With regard to the lower incisors Broom (1915b) recorded 3 and Broom (1932) 4. Boonstra (1934) stated that there are 3 lower incisors. If there were 3 lower incisors, this specimen would be an early therocephalian, but the presence of 4 lower incisors would, on the other hand, indicate that it belongs with the Gorgonopsidae.

Neither Broom (1915b, 1932) nor Boonstra (1934) doubted that the specimen is a therocephalian and indeed Broom's (1915b) illustration portrays the lower part of the mentum as complete and without the gorgonopsian chin. There is no real evidence to contradict this view. The specimen is therefore regarded as a therocephalian and because of the presence of serrated teeth it would either be a scylacosaurid or a lycosuchid. Boonstra's (1934) count of 3 lower incisors is consequently accepted as correct. Because of its size the specimen is probably a juvenile but cannot be classified below the level of family.

Haughton (1924) included Cerdodon tenuidens in the Ictidosuchidae as did Boonstra (1934) who also pointed out that the specimen had no morphological or phylogenetic value. Romer (1945) placed it in the family Scaloposauridae whilst Haughton & Brink (1955) classified it with the Pristerognathidae. Romer (1956) included Cerdodon in the gorgonopsian family Galesuchidae although none of the then diagnostic features of the family can presently be seen on the specimen. Von Huene (1956) again regarded the specimen as a member of the Ictidosuchidae. Watson and Romer (1956) and Kuhn (1965) maintained the specimen as a gorgonopsian in the family Galesuchidae. Vjuschkov (1964) also regarded it as a gorgonopsian in the subfamily Galesuchinae. Boonstra (1969b) does not mention the specimen and Kitching (1977) correctly regarded Cerdodon tenuidens as a nomen dubium.

Cynariognathus gallowayi Broom, 1936

Holotype

TM 266.

Material

Scylacosaurid skull extensively weathered over its entire surface, lacking the occiput, left postorbital arch, left temporal arch, posterior portion of the left ramus of the lower jaw, middle portion of the right ramus of the lower jaw, and the right jaw articulation.

Locality

Luttig Siding, Beaufort West.

Collected

J.A. Galloway.

Original generic diagnosis

See holotype of *Cynariognathus platyrhinus* for generic diagnosis of *Cynariognathus*.

Original specific diagnosis

There are apparently 9 molars (after Broom 1936a:356).

References

Broom 1936a: 356, fig. 5

Kuhn 1937a: 121

Haughton and Brink 1955: 129

Kuhn 1965: 94

Boonstra 1969b: 57

Kitching 1977: 40

Comments (Fig. 45a-d)

Contrary to Broom (1936a) no part of the skull is well preserved. Both premaxillae contain 5 incisors with a diastema between the third and fourth tooth making 6 incisors on each side. The posterior edge of the sixth incisor on the

left is serrated as are the lower incisors. Both premaxillae are posteriorly overlapped by the maxillae up to the level of the fourth incisor.

In the left maxilla a single large canine is visible with an equally large diastema behind it which in turn is followed by the remains of 6 postcanines, serrated both in front and behind. Only the first postcanine is well preserved and, unlike the incisors, the posterior edge of the tooth is not bladelike but rounded.

In the right maxilla the remains of only 6 postcanines are visible and not 9 as noted by Broom (1936a). Anterior to the first postcanine on the right is an area of cancellous bone indicating where the root of the previously functional canine was resorbed in the posterior canine alveolus. Anterior to this the replacing canine is visible. In this specimen both functional canines lie in the anterior position although the left canine is further developed than the right one. According to Broom (1936a) the 9 postcanines measure 44mm. However, on both sides the 6 postcanines measure 35mm. Broom (1936a) figured the right view (his Fig. 5) of Cynariognathus gallowayi with 9 postcanines pointing out that the first postcanine is represented by a fragment of root only. In actual fact the real first postcanine lies on a fracture and has been counted as two teeth by him. Anterior to the first postcanine is a diastema and anterior to that lies the cancellous infilling of the resorbed root of the previously functional canine in the posterior canine alveolus

(see Van den Heever, 1980) with an anteroposterior measurement of 13mm. At the posterior border of the cancellous region a tiny sliver of bone (0,9mm in anteroposterior measurement) is present. Broom (1936a) probably regarded this sliver as the remains of the first postcanine and the natural diastema between the posterior canine alveolus and the real first postcanine as the position of the second postcanine. Regarding the fractured real first postcanine as two teeth brought Broom's (1936a) count for the postcanines up to 9 (Fig. 45d).

The symphysis is loose and forms a straight line with the ventral border of the lower jaw. Three lower incisors are present with a single large canine and eight lower postcanines in the right jaw ramus.

The position of the prefrontal is usual and it bulges slightly on the right side. The anterior extremity of the prefrontal is in line with the last postcanine. There is a slight preorbital depression with a shallow groove leading in the direction of the first postcanine. The configuration of the postfrontal is usual. The frontal forms the middle portion of the dorsal border of the orbit. The postorbital forms the middle portion of the postorbital bar.

The reason why the parietal foramen is large is that it is broken through below the dorsal surface of the parietals where the canal leading to the brain cavity widens. The septomaxilla is present but damaged. The frontoparietal suture is well interdigitated. The epipterygoid is

scylacosaurid in appearance and is widened dorsally. The parabasisphenoid keel is well developed and infraorbital fenestrae are present. The jugal forms the posteroventral border of the orbit.

This is a very poor specimen of which almost the entire outer surface of bone is missing. The large number of postcanines suggest that it is a member of the Scylacosauridae. Because it presumably possessed 6 upper incisors and bears no other diagnostic features it is here referred to Glanosuchus macrops.

Cynariognathus paucioridens Broom, 1954

Holotype

SAM 11560a

Material

Anterior half of badly weathered skull with most of right ramus and anterior half of left ramus of lower jaw: 3 weathered postcranial fragments and one dicynodont skull and lower jaw fragment.

Locality

Kroonplaas or Heuningkopsfontein, Beaufort West (see Kitching, 1977).

Collected

L.D. Boonstra

Original generic diagnosis

See Cynariognathus platyrhinus for generic diagnosis of Cynarioghaus.

Original specific diagnosis

Six closely packed postcanines occupying 27mm. (left) and 28mm. (right); breadth of snout over canines 50mm.; height of snout at posterior edge of canine 40mm.; preorbital length of skull 99mm.; maxilla long, low; lacrimal large; prefrontal fairly small; dentary fairly lightly built; preorbital groove fairly deep (after Boonstra 1954a:93).

References

Boonstra 1954a: 93, Fig. 11

Haughton and Brink 1955: 129

Kitching 1977: 39

Comments (Fig 46a-c)

Boonstra (1954a) noted that were it not for a second specimen (SAM 11586) with six closely packed postcanines, he would have hesitated in naming Cynariognathus paucioridens. Subsequent to the description of Boonstra the type had been treated with acid by persons unknown and what little information the specimen originally presented has

unfortunately deteriorated further. Probably at this time too the left ramus of the jaw was removed to afford a better view of the palate.

The palate is damaged but shows the choanae extending to the post-canine region. The characteristic pterygoid bosses are also present although no evidence of pterygoid teeth can be seen. Both maxillae show evidence of a canine in the anterior alveolus. Behind each canine is a short diastema of about 5 mm. Six closely packed post-canines are present in each maxilla but they are so damaged that little can be concluded about their nature. The premaxillae, septomaxillae, upper incisors and the anterior parts of the nasals have been weathered away.

The mentum slopes posteriorly and the ventral margin of the symphysis is straight as is usual in the Therocephalia. The root of the lower canine is present as well as the partial roots of 3 incisors. The specimen is of no diagnostic value but because of the length of the internal choana and the relatively large number of postcanines it may be placed as Scylacosauridae <u>incertae sedis</u>.

Cynariognathus paucioridens Boonstra, 1954

Referred specimen

SAM 1080

Material

Extremely badly weathered fragment of a therocephalian skull and associated pes with a phalangeal count of 2,3,3,3,3.

Locality

Fraserburg Road (Now Leeu Gamka Station, Prince Albert).

Collected

J.H. Whaits.

References

Boonstra 1954a: 94

Kitching 1977: 36

Comments

The lower jaw is slender and appears to have a sloping mentum. The remains of a single canine is visible in the right maxilla. Contrary to Boonstra (1954a) the roots of eight postcanines and not 7 are visible in section in the left

maxilla. The provisional inclusion originally by him of this specimen as Cynariognathus paucioridens of which the most prominent feature is supposed to be the presence of 6 closely packed postcanines, is therefore incorrect.

SAM 1080 is so badly weathered that the only suture visible is that between the frontals. Evidence of a preorbital depression is visible on the right side.

Because of its poor condition this specimen is of no diagnostic value whatsoever and is here regarded as Therocephalia incertae sedis.

Cynariognathus paucioridens Boonstra, 1954

Referred specimen

SAM 11586

Material

Extremely badly weathered scylacosaurid snout with anterodorsal portion of lower jaw.

Locality

Koedoeskop, Beaufort West.

Collected

L .D. Boonstra.

References

Boonstra 1954a: 94

Kitching 1977: 39

Comments

Boonstra (1954a) expressed some doubt as to the validity of the type of Cynariognathus paucioridens and stated that if it were not for this second specimen with 6 closely packed postcanines he would have hesitated in naming the type.

The second specimen, SAM 11586, is extremely poor. The canines appear to be in the anterior alveoli. In the right maxilla 5 post-canines are present and in the left 6. The lower jaw has been sheared off ventrally and the roots of 4 postcanines can be seen in the right ramus and three in the left. One canine root and a single incisor are visible in each lower jaw ramus.

As the result of damage to the premaxillary region the total number of incisors can only be estimated but, the roots of 4 incisors are visible on the left and 5 on the right. In all probability there were at least 6 incisors in each premaxilla. The most anterior incisor in the right premaxilla has a replacement tooth behind it. As the result of weathering no serrations are visible on any tooth in this specimen.

However, additional doubt is cast on the validity of Cynariognathus paucioridens since the referred specimen SAM 11586 was also referred to the genus Pristerognathus by Boonstra (1954a:87) because it possessed 6 upper incisors occupying a space of 35 mm. As the total number of incisors cannot be definitely determined it is possible that SAM 11586 was mistakenly included as Pristerognathus. The tooth bearing area anterior to the canine does, however, appear to comprise approximately 35mm.

The symphysis of the specimen is loose and what can be seen of the ventral margin of the lower jaw indicates that it was straight as is usual in the Therocephalia. Because of the large number of postcanines and the probability that the specimen did possess 6 upper incisors it is regarded as Scylacosauridae incertae sedis.

Cynariognathus platyrhinus (Broom), 1912

Holotype

AMNH 5502

Material

Fragmentary anterior portion of a badly weathered scylacosaurid snout and lower jaw.

Locality

Grootfontein, Beaufort West.

Collected

J. H. Whaits.

Original generic diagnosis

See holotype of Pristerognathus polyodon for generic diagnosis of Pristerognathus.

Emended generic diagnosis

It cannot belong to Pristerognathus as it has 8 molars, nor can it belong to Alopecognathus as it is evidently a short broadheaded form (after Broom, 1931: 161).

Original specific diagnosis

The snout is broad and flat, and the lower jaw is comparatively straight and with very little of the usual upcurving in the canine and incisor region (after Broom, 1912: 863).

Emended specific diagnosis

As for original specific diagnosis

References

Broom 1912: 863-864, Plate XCI Fig. 8

Broom 1914: 47, Plate 6 Fig. 73

Broom 1915a: 119

Haughton 1924: 77,101

Broom 1931: 161

Broom 1932: 57, Fig. 18C-D

Boonstra 1934: 216

Boonstra 1935a: 6

Broom 1936a: 356

Kuhn 1937a: 121

Haughton & Brink 1955: 129

Kitching 1977: 36

Comments (Fig. 47a-d)

Broom (1912) provisionally included this specimen in the genus Pristerognathus because he regarded it as '...probably from near the same horizon...' as Seeley's (1895) holotype of Pristerognathus polyodon, and because the arrangement of the incisors was, to him, sufficiently similar in the two specimens. However, Broom (1931) placed it in a new genus Cynariognathus because it possessed 8 postcanines as opposed to 6 in Pristerognathus.

Broom (1912) noted that there were apparently 6 upper incisors. In (1932) he recorded 6 well developed upper incisors. According to Boonstra (1935a) there are 3 upper

incisors on the right and 4 on the left, with space on each side for possibly 5 teeth only.

The specimen lacks the anterior portions of the premaxillae and the number of upper incisors is therefore indeterminate. In the right premaxilla the roots of the 3 hindmost incisors are preserved and in the left premaxilla, the roots of the 4 hindmost teeth. In front of the anterior tooth in the left maxilla is an impression of what was probably an additional incisor. Between this impression and the approximate medial border of the premaxilla is a space which may have housed another tooth. The probable number of upper incisors appears therefore to have been 6.

Neither Broom (1912, 1932) nor Boonstra (1935a) could find positive evidence of tooth serrations. However, the largest postcanine in the right jaw ramus is preserved as an impression in which tooth serraitons are present.

According to Broom (1912) there are probably three lower incisors. The lower jaw is impacted into the upper and Boonstra (1935a) correctly pointed out that the lower incisors are hidden from view by the upper jaw.

There are 8 postcanines in the left maxilla and right lower jaw ramus as noted by Broom (1912) and Boonstra (1935a). The right jaw ramus is broken behind the eighth tooth and it is therefore possible that more teeth may have been present in life.

According to Broom (1912) the snout is broad and flat, and according to Broom (1932) short. Boonstra (1935a) described the snout as low and broad. The roof of the snout is however weathered off and together with the missing anterior portions of the premaxillae the snout has a blunt appearance. The snout is however too fragmentary to base any diagnosis on its shape.

An interesting point in the figure given by Broom (1914) of the specimen is that a definite crista choanalis is illustrated on the medial surface of the maxilla in the canine region. This can clearly be seen on the specimen as well. Boonstra (1935a) pointed out that the canines are rounded in section with no evidence of serrations. However, the canines are present only as sections at the gumline.

Broom (1932) included this specimen in a new genus viz. Cynariognathus, diagnosed by 8 postcanines as opposed to 6 in Pristerognathus. He also noted that the specimen could not belong to Alopecognathus since it was a short, broadheaded form. The holotype of Alopecognathus has however been subjected to strong lateral compression whereas the holotype of Cynariognathus platyrhinus has been dorsoventrally compressed as is shown by the way the lower jaw is compacted into the palate and the preorbital depression is enhanced.

Boonstra (1935a) correctly pointed out that nothing can be determined of the palate with any certainty. A suborbital fenestra is, however, present.

Cynariognathus platyrhinus is an early therocephalian because it has serrated teeth. The distinct crista choanalis medial to the canine indicates that it belongs in the Scylacosauridae. However, since it evences no additional features by which it can be diagnosed below the level of subfamily, it is here regarded as a nomen dubium.

Cynariognathus platyrhinus Broom, 1912

Referred specimen

BMNH R4097

Material

Badly weathered and laterally crushed snout of a scylacosaurid therocephalian.

Locality

Uitkyk, Prince Albert.

Collected

Unknown (Catalogue in British Museum reads: Purchased from T. Bain).

References

Boonstra 1934: 216-217

Boonstra 1935a: 6

Kitching 1977: 45

Comments

This specimen is very poorly preserved. Boonstra (1934) recorded 2 anterior and 2 posterior upper incisors with space of an additional tooth between. However, the anteriormost of these teeth is actually located in the lower jaw as the first tooth in the left ramus. Because of the fragmentary nature of the specimen and the sections cut from it by Boonstra (1934), the exact number of incisors are indeterminate, but there were probably at least 7 of which some show serrations. At least 7 postcanines are visible in the right lower jaw ramus. The number of lower incisors is indeterminate.

The sections of the specimen were cut in the postcanine region and not in the anterior part of the snout as stated by Boonstra (1934). The vomers are usual for a scylacosaurid in that they are not expanded anteriorly as in the Euchambersiidae (see Hopson and Barghusen 1986). According to Boonstra (1934) the vomers are fused posteriorly and unfused anteriorly. This observation is incorrect as the vomers are completely unfused.

Because serrations are present on the teeth, this specimen is either a gorgonopsian or an early therocephalian. The unfused vomers indicate that it definitely belongs to the

latter taxon. No other diagnostic features are present save the large number of postcanines. BMNH R4097 is therefore regarded as Scylacosauridae *incertae sedis*.

Cynariognathus seeleyi Broili and Schröder, 1936.

Holotype

UM 1934 VIII 30

Material

Badly weathered and laterally compressed skull of a scylacosaurid therocephalian with partial lower jaw and 4 cervical vertebrae; without right postorbital portion of the skull.

Locality

La-de-da, Beaufort West.

Collected

G. Grossarth.

Original generic diagnosis

See holotype of *Cynarioganthus platyrhinus* for generic diagnosis of *Cynariognathus*.

Original specific diagnosis

Skull narrow, slender and with long preorbital region; diameter of orbit small with orbit almost completely in posterior half of skull; size and relative positions of constituent bones as in typical pristerognathids; postfrontal clearly developed between frontal and postorbital; in contrast to condition found in closely related therocephalians, post-orbital extends posteriorly to beyond level of parietal foramen; canine strong; incisors nearly as long as postcanines; diastema between last incisor and canine relatively large; incisors and postcanines, and probably also canines, posteriorly serrated; tooth formula I.5,C.1,Pc.8 (after Broili and Schröder 1936a: 18-19).

References

Broili and Schröder 1936a: 1-20, Figs 1-5

Haughton and Brink 1955: 130

Kuhn 1965: 94

Boonstra 1969b: 57

Kitching 1977: 40

Comments (Fig. 48a-c)

This specimen was not seen in the original but is discussed on the basis of an excellent set of photographs from the files of the late Dr Christianne Mendrez-Carroll and the

original description of Broili and Schröder (1936a) who, in spite of the very poor material, succeeded in describing the type of Cynariognathus seeleyi in great detail.

The precanine region is badly damaged and the snout in this area is largely preserved as an impression. The incisor row is incomplete on both sides and the original number of incisors can therefore not be determined. Broili and Schröder (1936a) regarded the number of incisors to have been 5 in each premaxilla although it is clearly stated that in the right premaxilla the first and second incisors are present in a space of 10mm followed by a diastema of 10mm in which one alveolus can be seen. Next to the alveolus is a diastema of 4mm and finally 2 more teeth occupy a space of 11mm.

On the left the first incisor is 5mm wide at the base of its crown, then follows a diastema of 12mm which probably contained two teeth. Finally there follow 2 more teeth which occupy a space of 12mm. Between the last incisor on each side and the canine there is a diastema of 15mm.

From what can be seen in the left premaxilla it seems possible that there may have been 6 or 7 incisors present since it is not possible to determine with certainty that the last incisor on each side is actually the hindmost tooth. Because all the crowns measured a width of about 5mm it is probable that in the diastema of 14mm following the second incisor on the right, more than one tooth would probably have been present.

The right maxilla contains 8 postcanines and has a preorbital depression. The lateral surfaces of both maxillae are rugose. According to Broili and Schröder (1936a) the postorbital extends posteriorly beyond the parietal foramen.

Broili and Schröder (1936a) pointed out that the size and relative positions of the constituent bones in Cynariognathus seeleyi are as in typical scylacosaurids (pristerognathids). They erected the taxon by direct comparison with the published descriptions and measurements of Alopecognathus angusticeps (Broom 1915a, 1932; Boonstra 1935a), Pristerognathus vanderbyli (Broom 1925), Pristerognathus minor (Haughton 1918), Pristerognathus polyodon (Seeley 1895) and Cynariognathus platyrhinus (Broom 1912). Because these specimens are weathered and distorted it is not always possible to determine exact measurements and consequently relatively small differences in overall dimensions are therefore meaningless.

The specific diagnosis of Cynariognathus seeleyi is based on generalised scylacosaurid features. The one interesting feature is the posterior extent of the postorbital. It is not, however, diagnostic since it is also present in the holotype of Ptomalestes avidus. In scylacosaurids the posterior extremity ofthe postorbital is a thin vertical lappet of bone lying against the lateral surface of the parietal. It is therefore easily damaged and in most

specimens it original extent is difficult to determine. In specimens where it can be clearly seen, it usually extends to a point at least level with the parietal foramen. It is possible that the posterior margin of the bone may have been misidentified by Broili and Schröder (1936a) but even if the bone was correctly described by them, it would be unwise to regard any posterior increment as diagnostic since it reflects an essentially primitive condition.

The skull has an overall slender aspect and probably possessed at least 6 incisors. Because of these features it is fairly certain that the specimen belongs in the Scylacosauridae but cannot be classified beyond that. Cynariognathus seeleyi is therefore a nomen dubium.

Cynariognathus sp.

Referred specimen

SAM 3713

Material

Badly weathered anterior portion of a scylacosaurid snout.

Locality

Bloukrans, Prince Albert.

References

Boonstra 1954a: 94

Kitching 1977: 33

Comments

A poor snout with 6 incisors, 1 canine and at least 4 postcanines. Since the specimen is broken through the postcanine region the original number of postcanines are indeterminate. Although the dentition is badly damaged, serrations are visible on some teeth. The specimen is therefore a scylacosaurid and because of the number of incisors and lack of precanines, referred to Glanosuchus macrops.

Cynariognathus sp.

Referred specimen

SAM 9088a

Material

Weathered snout fragment of an early therocephalian with matching fragment of lower jaw.

Locality

Kleinkoedoeskop, Beaufort West.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 94

Kitching 1977: 38

Comments

The sloping mentum, loose symphysis with a straight ventral margin and the presence of tooth serrations all indicate that the specimen is an early therocephalian. The two fragments are, however, so poor that they are of no diagnostic value whatsoever and the specimen is therefore regarded as early Therocephalia *incertae sedis*.

Cynariognathus sp.

Referred specimen

SAM 11968

Material

Badly weathered snout of a scylacosaurid therocephalian with two weathered vertebrae probably belonging to a larger animal.

Locality

Unknown.

Collected

Unknown.

References

Boonstra 1954a: 94.

Comments

The vomers are unfused indicating that the specimen is an early therocephalian. There are 6 incisors in each premaxilla and the maxillae lack precanines. The specimen is therefore referred to Glanosuchus macrops.

Eriphostoma microdon Broom, 1911

Holotype

AMNH 5524

Comments

Two portions of a small damaged skull considered by Broom (1911, 1915a) to be a therocephalian but placed in the Gorgonopsia by Haughton (1924). Williston (1925) and Broom

(1932) doubtfully retained the specimen amongst the early Therocephalia. Boonstra (1935b) regarded it as a gorgonopsian as did most subsequent authors viz. Romer (1945, 1956), Haughton & Brink (1955), Watson & Romer (1956), Lehmann (1961), Vjuschkov (1964) and Boonstra (1969b). Von Huene (1956) placed it in the Pristerognathidae. Sigogneau (1970) considered the specimen as Theriodontia incertae sedis, a view also reflected by Kitching (1977).

The specimen has 4 lower incisors, serrated teeth and from what remains of the occiput and dorsal skull roof it is clear that the intertemporal region is wide. The mentum is steep and shows the gorgonopsian chin. Eriphostoma microdon is therefore definitely a gorgonopsian.

Glanosuchus macrops Broom, 1904

Holotype

SAM 637

Material

Skull and lower jaw of a large, weathered and slightly crushed scylacosaurid lacking the anterior portions of the nasals, nasal processes of the premaxillae, left postorbital arch, left temporal arch, most of the right postorbital and

temporal arches, both squamosals, the lateral portions of the occiput, the postdentary bones of both lower jaw rami as well as the middle portion of the left ramus.

Locality

Knofloksfontein, Beaufort West.

Collected

J. P. Snyman.

Original generic diagnosis

The dentition differs from that of any of the therocephalians in which the full dentition is known; there are 5 large, pointed, sub equal incisors on each side, each with a flattened and finely serrated posterior border; behind the fifth incisor is a small pointed tooth which I regard as a sixth incisor; a single large canine; apparently 5 small molars (after Broom 1904a: 86).

Emended generic diagnosis

Large pristerognathids with dental formula I.5+1,C.1,Pc.5; first 5 incisors large but sixth inconstant and when present very small; canine large and strong; postcanines moderately to weakly developed; skull large (max. length 315-321); preorbital hollow fairly shallow, not sharply

demarcated and really not more than a groove stretching from the orbit in the direction of the canine; septomaxilla and septomaxillary foramen well developed; snout broader than high, slightly narrowed between orbit and canines; orbits well in posterior half of skull; mandibular symphysis formed solely by dentaries, weak, unankylosed, mentum sloping; epipterygoid only slightly widened; sagittal crest of parietals only moderately high but fairly sharp (Boonstra 19544a: 75).

Original specific diagnosis

As for genus.

Emended specific diagnosis

As for genus.

References

Broom 1904a: 85-87, Plate VI fig. 1-6

Haughton 1924: 76, 101

Broom 1932: 60, Fig. 20A+B

Kuhn 1937a: 123

Von Huene 1938: 310

Romer 1945: 602

Boonstra 1954a: 75-78, Fig. 4

Haughton & Brink 1955: 130

Kitching 1977: 39

Comments (Fig. 49a-d)

Broom (1904a) erected Glanosuchus macrops solely on features of the dentition whereas Boonstra (1954a) included numerous generalised scylacosaurid features in his emended generic diagnosis. As in the case of Scylacosaurus sclateri Broom (1904a) mistook the septomaxilla for a process of the premaxilla. The region around the external nares is too badly damaged to allow accurate description. Consequently the size of the external nares cannot be as accurately determined as indicated by Broom (1904a). He also commented on the concave frontal region of the specimen. This condition is generally present in scylacosaurids and may be enhanced in mature skulls where there is a thickening of the dorsal borders of the orbits. The remainder of Broom's (1904a) description is essentially correct, but applies to scylacosaurids in general and is not specifically unique. An interesting point, however, is the distribution of the pterygoid teeth on the palate. There are no teeth on the ventral rim of the transverse processes of the pterygoids, but both of the pterygoid bosses show the roots of a number of small teeth. The boss on the left seems nearly complete and has the roots of at least 13 teeth implanted in it. It is situated diagonally on the palate, extending from the midline, immediately anterior to the proximal portion of the transverse

process of the pterygoid, to the posteromedial border of the suborbital fenestra.

Extending anteriorly from each pterygoid boss is a slightly divergent pterygo-palatine ridge. This ridge is present in all specimens in which the palate is preserved i.e. the holotypes of Ptomalestes avidus and Scylacosaurus sclateri. In Glanosuchus macrops SAM 637 the left pterygo-palatine ridge is very prominent and appears to have beens somewhat enhanced by distortion. What appears to be the root of a single tooth is situated in this ridge. A small pterygoid crest is present in the ventral midline between the two pterygoid bosses (Fig. 49d) as in the advanced Therocephalia and certain scylacosaurids viz. Pristerognathoides vanderbyli MM 5139 and Alopecognathus angustioriceps SAM 9342.

There are six serrated incisors in each premaxilla. The serrations occur both anteriorly and posteriorly on the teeth and vary in position on each tooth in relation to the curvature of the snout (Fig. 27).

In each maxilla a single, posteriorly serrated canine is visible in the anterior canine alveolus.

In the right maxilla 4 serrated postcanines are present with a diastema for an additional postcanine between the third and fourth tooth.

Boonstra (1954a) emended the generic diagnosis and referred an additional three specimens to the genus. His

measurement of the type skull (max. length 315-321mm) is correct and on both sides the preorbital depression is a shallow hollow. On the right a groove leading to the canine position is discernable, but may have been enhanced through distortion.

The septomaxilla and maxillo-septomaxillary foramen, although damaged, appears usual. Boonstra (1954a) noted in his diagnosis that the frontal enters the orbital border. This feature is, however, common to all therocephalian taxa except certain whaitsiids. The postfrontals are damaged but appear normal. The snout is broader than high and slightly narrowed between the canines and orbits as in all Scylacosauridae and is therefore not diagnostic at generic level.

Contrary to Boonstra (1954a) the mandibular symphysis is formed not just by the dentaries but also by the anterior extremities of the splenials as in all early therocephalians. This feature is also evident on both referred specimens. The unankylosed symphysis and the sloping mentum is charcteristic of the Therocephalia as a whole.

Both epipterygoids are badly damaged but from what is visible it is clear that they conform to the condition found in the early Therocephalia. The dorsal portions of the parietals and the squamosals are missing and consequently nothing can be said about the sagittal crest of the specimen.

Boonstra (1954a) also included an extensive description of this specimen, all of which consisted of generalised, early therocephalian features. Contrary to his statement that the lateral surface of the maxillary is smooth the left maxilla can be seen to be rugosely pitted. The pits are, however, filled with matrix. The right maxilla still has a thin covering of matrix partially obscuring the rugosities which can only be seen on closer inspection.

Because Glanosuchus macrops SAM 637 possesses teeth on the pterygoid boss it may be referred to the Scylacosauridae. However, it is also the earliest specimen described as having 6 upper incisors and no precanines. These features are here regarded as diagnotic and for that reason Glanosuchus macrops is deemed valid.

Glanosuchus macrops Broom, 1904

Referred specimen

SAM 903

Material

Very badly weathered anterior portion of a scylacosaurid snout and lower jaw.

Locality

Seekoeigat, Prince Albert.

Collected

P. H. du Plessis.

References

Boonstra 1954a: 78

Kitching 1977: 43

Comments

This snout fragment is so weathered that it is of little interest. Three lower incisors are visible in the left jaw ramus and the remains of 6 upper incisors are present in each premaxilla. On the right the last incisor is considerably smaller than the fifth but on the left the last incisor is in

fact quite large and only slightly smaller than the second last tooth. There are no precanines.

The features exhibited by this specimen conform with those found in scylacosaurids with 6 upper incisors and it is therefore retained as Glanosuchus macrops.

Glanosuchus macrops Broom, 1904

Referred specimen

SAM 11843

Material

Badly weathered and crushed scylacosaurid skull, lacking both lower jaw articulations, right coronoid process and postdentary bones, most of the anterior half of the left lower jaw ramus, most of the left maxilla, lacrimal and prefrontal as well as most of the squamosals and the occiput.

Locality

Lammerkraal, Prince Albert.

Collected

L. D. Boonstra.

References

Boonstra L.D. 1954a: 78, Fig.5

Kitching 1977: 40.

Comments

Boonstra (1954a) referred this specimen to Glanosuchus macrops because, according to him, the frontal has a small entry into the orbital border, the postfrontal and postorbital flank the parietal for a short distance within the temporal fossa, the parietal crest is not very high, but sharp and the temporal fossa short, but roomy. The area under consideration is badly damaged but the above features mentioned by Boonstra (1954a), which is complementary to the condition in the holotype, are not mentioned in the diagnosis of the genus and are all generalised early therocephalian characters.

Boonstra (1954a) regarded the temporal fenestra as short but roomy. It is too damaged to permit precise measurements but in comparison with other skulls appears usual for scylacosaurids in that its anteroposterior measurement equals about one third of the overall skull length. No objective statement can be made about the width of the temporal fossa but it does not seem unusually wide. Boonstra (1954a, Fig. 5) also illustrated 5 well spaced postcanines in the right maxilla which according to him are smaller than in the holotype SAM 637. The postcanine region of the left maxilla is missing but additional preparation of the right maxilla has revealed the existence of a single serrated postcanine and the probable root of a second tooth, neither of which is appreciably smaller than the postcanines of the holotype.

According to Boonstra (1954a) the occiput is less deeply concave than in the type, the preorbital depression shallow and the maxilla smooth over the canine bulge. Since the occiput of the specimen is so badly damaged, a statement of this kind cannot be made objectively. The right maxilla, and what is left of the left maxilla, have been weathered superficially, and consequently no statement can be made as to whether these bones were smooth or rugose on their outer surfaces. It does appear however that the preorbital depression was shallow, with a shallow groove extending from it in the direction of the base of the canine.

There are 5 widely spaced incisors in the right premaxilla. The fourth tooth seems slightly dislocated and an additional tooth was probably present behind it. The left premaxilla also contains 5 teeth together with a large diastema for an additional tooth behind the second incisor.

The remains of a canine and at least 3 postcanines are present in the remnant of the left lower ramus of the jaw.

The anterior portion of the left angular is preserved and, although very fragmentary, seems to possess a postdentary foramen. This feature is shared by all members of the early Therocephalia and foreshadows the development of the postdentary fenestra of the later therocephalians.

Because of the probable presence of 6 upper incisors and lack of precanines this specimen is provisionally retained as Glanosuchus macrops.

Glanosuchus macrops Broom, 1904

Referred specimen

SAM 11964

Material

Badly weathered partial snout and anterior portions of both lower jaw rami of a scylacosaurid therocephalian.

Locality

Unknown.

Collected

Unknown.

References

Boonstra 1954a: 78.

Comments

This specimen is badly weathered but shows 6 incisors in each premaxilla. Contrary to Boonstra (1954a) the sixth incisor on each side is only slightly smaller than the fifth.

The anterior extremity of the splenial is distinct and forms the ventral portion of the symphysis. In this point the specimen disagrees with the generic diagnosis of Boonstra (1954a). Since all the other characters of the genus, except

for the teeth, refer to skull parts not present on this specimen there is no way that it can be included in the genus on the basis of the diagnosis of Boonstra (1954a).

In a section through the palate behind the second upper postcanine the posterior portion of the vomer can be seen to underlie the palatine on the midline. Since the dorsal portion of the snout is missing all that can be said about this specimen is that it is a scylacosaurid with six upper incisors. It is therefore regarded as Glanosuchus macrops.

Glanosuchus macrops Broom, 1904

Referred specimen

GS M796

Material

Laterally compressed but nearly complete scylacosaurid skull lacking only the right temporal arch and left ramus of the lower jaw; with portions of 3 cervical vertebrae and distal part of ?radius.

Locality

Booiskraal, Beaufort West.

Collected

A. Chuma

Comments (Figs 1,2,3,6,10, 14-19, 23a-b, 24,25,50 a-b)

This skull is extremely well preserved and because it shows a large amount of detail, a general description of the anatomy was included in Chapter 4. An interesting feature of the specimen is that the median portions of the pterygoids, separated from the skull as a unit prior to fossilisation, was embedded directly below the cervical vertebrae. After detailed preparation it was possible to refit these elements exactly in place onto the skull.

The specimen has an elongated snout, long choanae and a number of teeth on each pterygoid boss. Although the root of a single tooth is visible proximally on the transverse process of each pterygoid, the ventral margins of the processess are devoid of teeth. The basal tubera are small and the skull base immediately below the sella turcica is narrow. At least 7 upper postcanines were present.

GS M796 is definitely a scylacosaurid and because it possesses 6 upper incisors but lacks precanines it is referred to Glanosuchus macrops.

Hofmeyria atavus Broom 1935

Holotype

TM 254

Material

Very small, nearly complete therocephalian skull, slightly crushed obliquely; with proatlas, atlas, axis and part of the third cervical vertebra.

Locality

Kookfontein, Victoria West.

Collected

R. Broom.

Original generic diagnosis

Skull small; I.5,C.1,Pc.5; maxilla shorter than in any other known therocephalian; postfrontal well developed; frontal excluded from the dorsal border of the orbit by the prefrontal and the postfrontal; dentary slender and curved (after Broom 1935a: 55-59).

Original specific diagnosis

As for genus.

References

Broom 1935a: 55-59, Fig. 1

Broom 1936c: 25-30, Figs 109-120

Kuhn 1937a: 133

Romer 1945: 602

Haughton and Brink 1955: 130

Romer 1956: 698

Von Huene 1956: 318, Fig. 365

Watson and Romer 1956: 70

Lehman 1961: 236, Fig. 12

Vjuschkov 1964: 280

Kuhn 1965: 105

Kitching 1977: 58

Comments (Fig. 51a-d)

This specimen has, on the whole, been regarded by previous authors as belonging either with the Alopecopsidae (Romer 1945, Von Huene 1956) or the Whaitsiidae (Romer 1956, Watson & Romer 1956, Lehman 1961, Vjuschkov 1964, Kuhn 1965). Haughton and Brink (1955) regarded it as a pristerognathid, as did Kitching (1977) albeit doubtfully.

The specimen is much smaller than any known mature early therocephalian and exhibits a number of advanced characters viz. incisors and canines striated and not serrated; the coronoid process of the dentary overlaps the anterior portion of the surangular extensively; the surangular and angular emarginated to form a postdentary fenestra and posttemporal fossa present in the opisthotic.

Hofmeyria shares the above features with all the later Therocephalia but still retains primitive features, also present in the early Therocephalia such as separate, unfused vomers and a well-developed postfrontal. Because of this Hopson and Barghusen (1986) regard Hofmeyria atavus as the most primitive member of the later Therocephalia and they

place it in the family Hofmeyriidae.

Hyaenasuchus whaitsi Broom, 1908

Holotype

SAM 1079

Material

Badly weathered but nearly complete skull of a large lycosuchid therocephalian with a large piece of matrix containing at least three cervical vertebrae.

Locality

Rietfontein, Prince Albert.

Collected

J. H. Whaits.

Original generic diagnosis

Differs from Lycosuchus in having 6 incisors and 4 molars instead of 5 incisors and 1 molar; rather larger than Lycosuchus vanderrieti, skull length 280mm and greatest breadth 152mm (after Broom 1908a: 364).

Emended generic diagnosis

Dental formula I.6,C.2,Pc.4; both canines large (after Haughton & Brink 1955: 135).

Original specific diagnosis

As for genus.

Emended specific diagnosis

As for genus.

References

Broom 1907c: 1053

Broom 1908a: 364-366. Plate XLVI Fig. 1

Haughton 1924: 76, 101

Broom 1932: 52-53, Fig. 16C

Kuhn 1937a: 119

Von Huene 1938: 310

Romer 1945: 602

Romer 1956: 698

Haughton and Brink 1955: 135

Von Huene 1956: 315,316,319, Fig. 367

Watson and Romer 1956: 69,88

Lehman 1961: 233, Fig. 6B

Boonstra 1963: 178

Vjuschkov 1964: 277

Kuhn 1965: 102

Romer 1966: 373

Boonstra 1969b: 53,57,61

Kitching 1977: 42

Comments (Fig. 52a-e)

This specimen consists of a virtually complete skull of which especially the dorsal and anterior surfaces of the snout have been badly weathered. The description of Broom (1908a) is correct but only lists the essentially early therocephalian features of the skull, rather than those features diagnostic at specific level. Unfortunately the specimen is preserved in extremely hard matrix and apart from a transverse break through the interpterygoid vacuity and another through the canine region the palate cannot be seen.

The incisor region is interesting in that an apparent discrepancy exists between the number of teeth in each premaxilla. The right premaxilla contains 5 large serrated teeth which fill the available space completely. Most of the left premaxilla is missing, but from the remaining tooth portions it seems that there may have been 6 incisors present. Because of the poor condition of the left premaxilla it is advisable not to attach too much importance to this aspect. Broom (1908a) figured the left premaxilla of this specimen with 5 teeth only.

In the right maxilla the large functional canine lies in the posterior alveolus with only the root of the previously functional canine in the anterior alveolus. In the left maxilla the large functional canine lies in the anterior alveolus. Contrary to Broom (1908a) the posterior canine on the left is not functional but should rather be regarded as the replacement of the functional canine (see Van den Heever,

1980). Four serrated postcanines are present in each maxilla, and, as in the holotype of Lycosuchus vanderrieti a lateral maxillary ridge is present below which the postcanines are implanted on the ventral maxillary flange.

The cross section through the canine region shows that the vomers are vaulted as in Lycosuchus vanderrieti GS M793 and Broom's (1936c) illustration of the lost type of Trochosaurus dirus (Fig. 83b). There is a slight preorbital depression on each side of the snout but without the diagonal groove extending towards the canine region. The suborbital bar is broad and in the transverse process of the left pterygoid four teeth are visible. Broom's (1908a) description of the skull roof is correct, with the exception that the bone meeting both parietals posteromedially is the interparietal and not the supraoccipital.

In ventral view the lower jaw is typically therocephalian in that the splenial lies flat against the dentary. The ventral margin thus forms a straight line with the symphysis. Anterior to the lower canine the roots of 5 teeth are visible in a ventral section of the jaw. Since the lower incisors are implanted at an angle, the outer three appear to be the functional incisors, whilst the two medial teeth are most likely replacements for the first and second incisors. Medial to the functional canine in the left ramus of the lower jaw its unerupted, serrated replacement is visible. The rest of the lower jaw is poorly preserved but appears usual for a member of the early Therocephalia. The angle of the jaw lies

approximately in line with the postorbital bar. Both angulars are damaged but the ridged pattern is still visible on the right. Broom (1908a) illustrated a large postdentary foramen in the left angular. The bone is, however, so damaged in this region that the structure cannot be seen and such an interpretation is therefore unjustified. Contrary to Broom (1908a) the right angular is badly damaged and not "almost perfectly preserved". His observations on the vertebrae appear correct.

Some confusion entered the literature after Broom (1932) misspelt Hyaenasuchus whaitsi as Hyaenosuchus whaitsi. Unfortunately this mistake was perpetuated by several subsequent authors viz. Kuhn (1937a), Von Huene (1938), Romer (1945), Romer (1956, index only), Boonstra (1963), Vjuschkov (1964) and Kuhn (1965). Von Huene (1956) not only misspelt Hyaenasuchus as Hyaenosuchus but on page 319, Fig. 367, he labeled the whaitsiid Hyenosaurus incorrectly as Hyaenosuchus.

Hyaenasuchus whaitsi strongly resembles Lycosuchus vanderrieti in general skull structure and in particular in the presence of a lateral maxillary ridge and a ventral maxillary flange. It is, however, not possible to determine the presence or absence of a vaulted vomer in Lycosuchus because the anterior portion of the palate is covered by the lower jaw and cannot be safely cleared of matrix.

Hyaenasuchus whaitsi is therefore deemed a junior synonym of Lycosuchus vanderrieti.

Hyorhynchus platyceps Seeley, 1889

Holotype

BMNH R872

Material

Badly weathered middle portion of a scylacosaurid skull without lower jaw.

Locality

Gouph Tract or Koup, Beaufort West.

Collected

T. Bain.

Original generic diagnosis

'It is characterised by a slender angular Pig-like snout, relatively large orbits and a narrow parietal region' (Seeley 1889: 242).

Original specific diagnosis

As for genus.

References

Seeley 1889: 242-243, Plate 15 Fig. 1-3

Broom 1932: 69

Boonstra 1934: 231

Kuhn 1937a: 127

Romer 1945: 602

Romer 1956: 697

Von Huene 1956: 316

Watson & Romer 1956: 69

Vjuschkov 1964: 276

Kuhn 1965: 94

Boonstra 1969b: 51

Kitching 1977: 36

Comments (Fig. 53)

Seeley (1889) described and figured Hyorhynchus platyceps. The specimen is extremely fragmentary and he identified the postorbital as the postfrontal. Because the teeth were lost Broom (1932) regarded the specimen as indeterminate, but considered it to be closely allied to Pristerognathus minor. Boonstra (1934) noted the presence of a well developed postfrontal and postorbital, a large parietal foramen and a narrow parietal region. He too regarded the specimen as a pristerognathid, taxonomically close to Pristerognathus.

Subsequent classifications all included Hyorhynchus platyceps within the Pristerognathidae (Romer 1945, Romer 1956, Von Huene 1956, Watson & Romer 1956, Vjuschkov 1964), although Romer (1956) and Watson and Romer (1956) were doubtful about the validity of the taxon. Boonstra (1969b) once again pointed out that the specimen is only identifiable

to family level.

The narrow intertemporal region and the presence of a postfrontal show that Hyorhynchus platyceps is an early therocephalian. The palatal region is long, like that of scylacosaurids and the relatively large orbit indicates that is is probably a juvenile.

Because of the poor condition of the specimen and the lack of diagnostic features below family level, Hyorhynchus platyceps is here regarded as a nomen dubium and is placed as Scylacosauridae incertae sedis.

Ictidoparia brevirostris Broom, 1925

Holotype

Lost, according to Broom (1932).

Material

Middle portion of a very small theriodont skull and lower jaw.

Locality

?Lammerkraal, Prince Albert.

Collected

Unknown.

Original generic diagnosis

Skull long and narrow; maximum length probably 62mm; nasals appear to have been narrow and prefrontals large; canine large and probably single; apparently 10 molars; frontals long and narrow; interorbital width 12mm; no distinct postfrontal but postorbital well developed; parietals small and apparently no high sagittal crest; pineal foramen small; mandible long and slender (after Broom 1925: 321-322).

Original specific diagnosis

As for genus.

References

Broom 1925: 321-322

Broom 1932: 66

Kuhn 1937a: 125

Romer 1945: 602

Haughton & Brink 1955: 130

Romer 1956: 697

Von Huene 1956: 316,321

Watson & Romer 1956: 69

Lehman 1961: 230

Vjuschkov 1964: 276

Kuhn 1965: 95

Boonstra 1969b: 51

Kitching 1977: 40

Comments

This little specimen was described by Broom (1925) but never figured. In 1932 he reported it lost. In spite of the small size of the specimen all previous authors regarded it as a pristerognathid, with the exception of Von Huene (1956) who placed Ictidoparia not only within the Pristerognathidae, but at the same time within the Ictidosuchidae as well. According to Boonstra (1969b) the specimen can only be identified to family level i.e. Pristerognathidae, a view also held by Kitching (1977). It must also be borne in mind that as the type has been lost since before 1932, all subsequent evaluations including this one have been based on the original description of Broom (1925).

The small size of the skull, the apparent lack of a postfrontal, the large number of postcanines, the lack of a sagittal crest, the small pineal foramen and the long slender mandible all argue against the specimen being a pristerognathid. There is also no mention of relatively large orbits which a juvenile pristerognathid presumably would have possessed, nor was anything said about serrations on any of the teeth. It is, however, possible that the teeth were so damaged that it was not possible to observe serrations, had they been present at all.

On balance therefore a plausible case can be made out that the specimen was after all not a pristerognathid but more probably a member of the advanced Therocephalia. In view of the meagre amount of information available about the specimen, but primarily becuase it has been lost, Ictidoparia

brevirostris is regarded as a nomen dubium.

Ictidosaurus angusticeps Broom, 1903

Holotype

SAM 630

Material

Very badly weathered anterior portion of a scylacosaurid snout with anterior portions of both lower jaw rami.

Locality

Near Beaufort West.

Collected

Presented by J.R. Joubert.

Original generic diagnosis

The snout is considerably deeper than broad; nostrils practically terminal; 5 incisors of moderate size with the fifth small; minute canine in front of large canine; probably 9 upper molars; 3 lower incisors and apparently 9 molars (after Broom 1903d: 151).

Emended generic diagnosis

The snout is deep and narrow and the nostril large; 5 fair sized pointed incisors followed by a very small sixth; canine

relatively large and sharp pointed with small, pointed, first canine in front of it; 8 small molars behind large canine (after Broom 1932: 60,62).

Original specific diagnosis

As for genus.

Emended specific diagnosis

As for genus.

References

Broom 1903d: 151-152, Fig. 4

Broom 1913a: 363

Broom 1913b: 230

Haughton 1924: 76,101

Broom 1932: 60,62,64, Fig.20E

Boonstra 1935a: 7

Kuhn 1937a: 123

Romer 1945: 602

Haughton & Brink 1955: 137-138

Romer 1956: 697

Von Huene 1956: 316,321

Watson & Romer 1956: 69

Lehman 1961: 230

Vjuschkov 1964: 276

Kuhn 1965: 95

Romer 1966: 373

Comments (54a-c)

This very poor specimen has a sloping mentum and a loose symphysis. It is therefore a therocephalian. The presence of three lower incisors and serrated teeth indicate that it is an early therocephalian. There are 6 upper incisors, the second represented by a diastema. Broom (1903d) stated, in his original diagnosis, the number of incisors to be 5 but later (1932) emended it to 6. In the right maxilla there are 6 postcanines with a diastema for an additional tooth in the third position. Immediately anterior to the first postcanine is a structure which may represent the root of a postcanine resorbed by the development of a previous canine in the posterior canine alveolus. In the left maxilla at least 6 postcanines are visible. Anterior to the functional upper canine is a single small marginal precanine. In the right ramus of the dentary there are at least 8 postcanines.

The nasal process of the premaxilla is seen to extend at least to the level of the posterior borders of the nares. The width of the snout over the canines is at least 41mm, which is also the approximate height of the snout. Since the specimen has been crushed considerably from side to side, Broom (1903d) is incorrect in stating that the snout is deeper than wide. All the other features of his diagnosis, with the exception of the small marginal maxillary precanine, is usual for early therocephalians. The large number of maxillary and mandibular

postcanines are not regarded as diagnostic at generic level and is most likely a function of the length of the snout.

SAM 630, incorrectly referred to as Ictidosuchus angusticeps by Broom (1913a), has had a chequered career with regard to taxonomy. Broom (1913b) suspected that it was a gorgonopsian. Haughton (1924) regarded it as a pristerognathid; Williston (1925) referred it to the Scylacosauridae, whilst Broom (1932) placed it in a new family, the Ictidosauridae, with Scylacosaurus, Scylacorhinus (=Scylacosaurus) and Akidnognathus. Romer (1945) referred it to the Scaloposauridae but later (Watson and Romer 1956, Romer 1956, Romer 1966) retained it in the Pristerognathidae. Haughton and Brink (1955) placed it in the Akidnognathidae, whereas Von Huene (1956) referred it to the Ictidosuchidae, a family regarded by him as ancestral to the Cynodontia. Lehman (1961) grouped the specimen with the Pristerognathidae but pointed out that it was insufficiently known and of doubtful affinity. Vjuschkov (1964) placed Ictidosaurus angusticeps in the family Scylacosauridae which, with the exception of Trochosuchus acutus, contained only those forms included in the family Akidnognathidae by Haughton and Brink (1955). Boonstra (1972) does not mention the specimen, but Kitching (1977) regarded it as a pristerognathid.

The possession of 6 upper incisors and 1 precanine is here regarded as diagnostic and since Ictidosaurus angusticeps was the first named specimen to exhibit these features, the taxon is deemed valid.

Ictidosaurus angusticeps Broom, 1903

Referred specimen

AMNH 5527

Material

Weathered, badly preserved and laterally crushed gorgonopsian snout.

Locality

Beaufort West, near base of *Endothiodon* Zone (after Broom 1915a: 118).

Collected

J. H. Whaits.

References

Broom 1915a: 118

Boonstra 1935a: 6-7

Comments (Fig. 55)

Broom (1915a) referred this specimen to the pristerognathid taxon *Ictidosaurus angusticeps*. Boonstra (1935a) considered it as unidentifiable and regarded it as a probable gorgonopsian. Since the specimen has 4 lower incisors,

serrated teeth and a deep upright mentum there is no doubt at all that it really is a gorgonopsian. It is also of interest to note that the locality lies outside the Tapinocephalus Zone (Broom, 1915a).

Karroowalteria skinneri Brink and Kitching, 1951

Holotype

BPI 220

Material

Dorsoventrally crushed preorbital portion of a large scylacosaurid skull with anterior and posterior portions of the left dentary and the anterior two thirds of the right jaw ramus.

Locality

Elandsfontein, Beaufort West (see comments).

Collected

A.J.W. Skinner.

Original generic diagnosis

The closest relatives of this genus are Pristerognathus and Scymnosaurus. It differs from Scymnosaurus in being of much larger size, having more molars and having the arrangement of the bones in the palate somewhat different. It differs from

Pristerognathus in being much larger and the snout much broader and more massive; the preorbital depression is specialised; Karroowalteria differs from both Pristerognathus and Scymnosaurus in having the snout broader in the canine region than immediately behind (after Brink and Kitching 1951: 1218-1220).

Original specific diagnosis

As for genus.

References

Brink and Kitching 1951: 1218-1222, Figs 1-3

Haughton and Brink 1955: 134-135

Rossouw 1955: 41

Romer 1956: 698

Von Huene 1956: 317

Watson and Romer 1956: 69

Kuhn 1958: 382

Lehman 1961: 231

Vjuschkov 1964: 276

Kuhn 1965: 101

Romer 1966: 373

Boonstra 1969b: 51,57

Kitching 1977: 35

Rubidge and Oelofsen 1981: 425

Comments (Fig. 56a-f)

This specimen was originally described by Brink and Kitching (1951) as Walteria skinneri. Kuhn (1958) pointed out that the name was preoccupied because of Mehl's (1931) usage and suggested the name Karroowalteria skinneri. Boonstra (1969b: 51) referred the specimen to the genus Pristerognathoides but on p.57 of the same article listed it as Alopecognathus skinneri, as did Kitching (1977). Rossouw (1955) pointed out that the original assignation of the locality to Vleifontein, Laingsburg was an error and that the real locality was Elandsfontein, Beaufort West.

The specimen has 6 upper incisors and no precanines. A single large canine is present in the anterior alveolus in both maxillae with a diastema behind each tooth. Contrary to Brink and Kitching (1951) there are 5 and not 6 postcanines in the right maxilla. In the left maxilla 4 postcanines are present with a diastema for another tooth between the third and fourth position. The third post-canine has been shed and in the alveolus the unerupted, serrated tip of the replacement tooth is visible, slightly medial to the position of the other teeth.

In the lower jaw three incisors, one canine and 6 postcanines are present. The symphysis is loose and the mentum slopes posteroventrally. The splenial is seen as a thin plate on the ventromedial surface of the dentary extending anteriorly into the ventral portion of the symphysis. The 6 postcanine roots in the lower jaw appear to alternate in size. The first, third and fifth appear equal

but smaller than the second fourth and sixth.

Brink and Kitching (1951) noted that in Karoowalteria the preorbital depression was 'specialised', as opposed to the condition in Pristerognathus and Scymnosaurus. This is incorrect since the condition in Karroowalteria is the result of dorsoventral crushing. In Pristerognathoides vanderbyli MM 5139 where the orbital portion of the skull roof is also dorsoventrally crushed the left preorbital depression is similar to that of Karroowalteria skinneri. The usual, oblique groove extends from the anteroventral margin of the depression towards the canine.

According to Brink and Kitching (1951) a character common to Karroowalteria, Scymnosaurus and Pristerognathoides (Pristerognathus) vanderbyli is the considerable height of the snout in the maxillary region as compared with the height in the orbital region. This feature is also said to be more pronounced in Karroowalteria. Unfortunately the skull roof in the orbital region is missing in Karoowalteria and the specimen is distorted to such an extent that in lateral view the ventral border of the orbit lies at the level of the apex of the snout. The height of the snout cannot therefore be compared with that of the orbital region.

Brink and Kitching (1951) also pointed out that Karroowalteria differs from all Pristerognathus and Scymnosaurus species in that the snout is broader in the canine region than immediately behind. This is a fallacy since in all members of the Scylacosauridae the canine region

is wider than the snout portion immediately behind it.

According to Brink and Kitching (1951) the canines extended well below the ventral border of the lower jaw. Since the canines are present as roots only this statment cannot be verified. This condition is not met with in any of the known early Therocephalia and does not take cognisance of the fact that in Karroowalteria the lower jaw is impacted into the palate to such an extent that the crowns of the postcanines remain impaled on the ventral surface of the palatine.

Figure 2 of Brink and Kitching (1951) shows the right ramus of the lower jaw situated too far posteriorly. The receding margin of the symphysis should actually lie anterior to the canine in lateral view. On the specimen it is clear that the right ramus of the lower jaw has been displaced backwards as the lateral indentation on the dentary for the crown of the upper canine now lies behind the fang.

The palate in Karroowalteria is damaged, but is of the usual scylacosaurid type. Immediately below the crista choanalis a sulcus is present which extends posteriorly, following the palatine-maxillary suture. The internal choanae are long and terminate posteriorly at a point in line with the second postcanine. Unfortunately as the result of distortion the vomers have been displaced dorsally, creating the impression that they form a vault. Anteriorly each vomer appears to possess a median groove. It is not clear whether this feature is real or whether it is the result of

distortion.

According to Brink and Kitching (1951) the vomer extends much further back in Karroowalteria than in either Pristerognathus or Scymnosaurus. This is incorrect since the posterior margin of the bone terminates at a point between the level of the last postcanine and that of the anterior margin of the suborbital vacuity as in all scylacosaurids where this portion of the palate is visible. The only specimen of Scymnosaurus in which part of the palate was preserved at the time was Scymnosaurus watsoni. This specimen has now been identified as a member of the Scylacosauridae and the palate is identical with that of Karroowalteria. It must also be borne in mind that the posterior margin of the vomer underlaps the anterior portion of the pterygoid and is of necessity a thin lamina of bone which may be easily damaged. In a specimen with a weathered palate it may therefore often appear shorter than it originally was. A pterygo-palatine ridge is present, terminating posteriorly in a pterygoid boss containing the roots of at least 6 teeth. No teeth are present on the transverse process of the pterygoid.

The presence of a crista choanalis, teeth on the pterygoid boss and the absence of teeth on the transverse process of the pterygoid indicate that Karroowalteria skinneri belongs to the Scylacosauridae. Because the specimen possesses 6 incisors and lacks precanines it is here referred to Glanosuchus macrops.

Lycedops scholtzi Broom, 1935

Holotype

MM 4499

Material

Badly weathered and posteriorly crushed scylacosaurid skull lacking middle portion of snout and lower jaw as well as most of the outer surface of the skull. The left postorbital bar is weathered away as well as the posterodorsal portions of the parietals and squamosals.

Locality

Abrahamskraal, Prince Albert.

Collected

C. S. Scholtz.

Original generic diagnosis

Clearly a near ally of *Pristerognathus* but differs in having only four molars. The front of the snout is much blunter and the temporal fossae broader and shorter than in *Pristerognathus*. The septomaxillaries divide the nostrils farther than in *Pristerognathus* (after Broom 1935b: 1-2).

Original specific diagnosis

As for genus.

References

Broom 1935b: 1-2, Fig. 1

Broom 1936c: 12,13,22-25

Kuhn 1937a: 133

Romer 1945: 602

Boonstra 1953b: 63

Haughton & Brink 1955: 130-131

Von Huene 1956: 316

Romer 1956: 697 Fig. 99E

Watson & Romer 1956: 69

Lehman 1961: 227

Boonstra 1963: 178

Vjuschkov 1964: 276

Kuhn 1965: 95

Romer 1966: 373

Boonstra 1969b: 52,57

Kemp 1972a: 11,14 Fig. 5a

Kitching 1977: 32

Comments (Fig. 57a-g)

Lycedops is so badly preserved that the exact skull length is indeterminate, but Broom's (1935b) estimate of 185mm appears reasonable. The dorsal portion of the occiput has been displaced anteriorly, shortening the temporal fenestra

anteroposteriorly. The lower portion of the occiput has resisted distortion because of its more robust build and consequently displays the relationships of the constituent bones reasonably well.

The remains of six, serrated, upper incisors are present in the premaxilla but it is not clear if this was the full complement of premaxillary teeth. The remains of what appears to be four upper postcanines can also be seen in the maxilla. According to Broom (1935b) the front of the snout is much blunter than in Pristerognathus. This is because in Lycedops the premaxillae have been weathered away anteriorly, exposing the remains of the incisor roots, whereas the anterior portions of the maxillae, flanking the premaxillae posteriorly, are still intact. The impression is thus created that the snout is bluntly rounded. Broom (1935b) also stated that the temporal fenestrae were broader and shorter than in Pristerognathus. This condition is the direct result of the anterior displacement of the dorsal portion of the occiput, as is evinced by the distorted aspect of the parietals and the squamosals.

The incisors are usual in that they increase in size from the first to the fourth and then decrease progressively. On the right, a fragment of bone, which may be the remains of a canine root, can be seen in the approximate position of the posterior alveolus. Broom (1935b) definitely regarded it as a second canine, but assumed that it was non-funcitonal and, by implication, distinguished between Lycedops and Lycosuchus,

the latter which he believed to have possessed two simultaneously functional canines in each maxilla. This aspect has been dealt with by Van den Heever (1980).

According to Broom (1935b) the nasals are short and the medial process of the septomaxilla divides the naris to a greater extent than in Pristerognathus. This is a subjective statement as the nasals are preserved only as impressions of which the middle portion is absent. At that time the medial process of the septomaxilla, because it is so fragile, was not completely preserved in any known specimen. In Lycedops it is preserved largely as an eroded impression which seemingly does not differ significantly from other scylacosaurids.

The anterior portion of the palate is destroyed but in ventral view a low, distinct, median crest (Fig. 57b) is visible on the posterior portion of the vomer, as in the holotype of Pristerognathus polyodon.

Contrary to Broom (1935b), neither the lacrimal nor its duct can be observed in the specimen. What he regarded as the anterior part of the lacrimal duct appears to be the impression of the contact between the anterolateral border of the nasal and the dorsal edge of the septomaxilla.

The skull roof is too damaged to describe the extent of the prefrontal, frontal, postfrontal and postorbital. All that can be said of these bones are that they were present in what appears to be their usual positions, together with the pineal foramen and a sagittal crest.

In the orbital region two thin, semi-circular bones,

identified by Broom (1936c) as presphenoids, form a trough directly below the frontals. These paired ossifications lie medial to the orbits, probably sheathed the olfactory lobes of the brain and may best be regarded as orbitosphenoids. They are too fragile to prepare but appear not to contact the ventral surface of the frontal and, contrary to Broom (1936c), do not meet ventromedially. In all probability a cartilaginous contact existed between the frontal and the orbitosphenoid.

Broom (1936c) described certain parts of the skull, notably the occiput, in greater detail. He also mentioned three small elements articulating with the ectopterygoid (his transpalatine) dorsally. This area is visible only in section on the specimen and the ectopterygoid can be seen to contact only the jugal. According to him a small element situated medial to the jugal articulates with the ectopterygoid and is probably the posterior process of the palatine. No such element is visible in the section as the contact between the posterolateral process of the palatine and the anterior process of the ectopterygoid lies anteroventral to the contact between the ectopterygoid and the jugal.

A fracture through the transverse process of the pterygoid has damaged the palate in the region of the interpterygoid vacuity. The roots of two small teeth are visible in the right pterygoid boss. The ventral margins of the transverse processes of the pterygoids are devoid of teeth but what appear to be the vestigial roots of two small teeth

are visible in seciton on each side, immediately lateral to the interpterygoid vacuity.

The section through the lower jaw in the region of the transverse processes of the pterygoid is comparable to that of other scylacosaurids.

The occiput of Lycedops is fairly well preserved but superficially weathered. The postparietal lies dorsal to the supraoccipital and between the tabulars. The contact between the tabular and the supraoccipital is indistinct but it appears that the dorsal process of the opisthotic meets the ventral margin of both these elements. A posttemporal fossa is not present in the paroccipital process but a distinct foramen is located at the base of the dorsal process of the opisthotic, medial to the posttemporal fenestra. Distally the mastoid process contacts the medial surface of the posterior squamosal ridge and the quadrate process meets the quadrate dorsomedially. Both the quadrate and quadratojugal are visible in posterior view. The former is an upright bone covered posterodorsally by the squamosal. Ventrally it forms a transverse roller which articulates with the lower jaw. The quadratojugal is also covered posterodorsally by the squamosal. A quadrate foramen is present between the quadrate and quadratojugal.

Dorsal to the quadrate foramen the squamosal appaears to be slitted, as pointed out by Broom (1936c). The posteroventral margin, as well as the posterior surface of both squamosals, are, however, weathered and it is not evident

if the configuration as illustrated by Broom (1936c) is real. In most specimens this region is damaged and the morphology is not distinct. From the condition in other specimens it appears that in scylacosaurids at least the squamosal is not as markedly cleft posteriorly as indicated by Broom (1936c). A possible explanation for the presence of the squamosal slit in weathered specimens is that the quadrate and quadratojugal are imbedded in a depression on the anterior face of the squamosal, with only a relatively thin lamina of bone covering them posteriorly. Weathering of the occipital surface of the squamosal would tend to destroy that portion of the squamosal not supported by the quadrate and quadratojugal, hence the slitted appearance of the squamosal between these two bones.

Distally the ventral surface of the paroccipital process is vaulted between the mastoid and quadrate processes. The ventral border of the squamosal between the two heads of the paroccipital process in this region is sharp and form a semi-circle around the concave ventral surface of the paroccipital heads (Fig. 57f). It appears, therefore, that if a tympanic membrane was present in the early Therocephalia, it would most probably have attached at this point, an opinion shared by Broom (1936c) and Boonstra (1954a).

Both stapes are intact and lie as two, fairly stout, dumbbell-shaped bones extending from the fenestra ovalis to the medial process of the quadrate roller. As in all Therocephalia a stapedial foramen is not present. Broom (1936c) interpreted the portion of the stapes situated dorsal

to the stapedial-quadrate contact as a stapedial process (Fig 57e). In view of the poor condition of the specimen this particular contact is considered an artefact of distortion.

The large number of incisors and small basal tubera indicate that MM 4499 is a member of the Scylacosauridae. Unfortunately the poor condition of the specimen precludes a definite statement about its taxonomic position. Lycedops scholtzi is therefore a nomen dubium and is here regarded as Scylacosauridae incertae sedis.

Lycosaurus pardalis Owen, 1876

Holotype

BMNH R1717

Comments

A gorgonopsian skull which Williston (1925) doubtfully referred to the Scylacosauridae and which was regarded by Broom (1932) as an early therocephalian. Sigogneau (1970) placed the specimen as Theriodontia incertae sedis.

Lycosuchus mackayi Broom, 1903

Holotype

SAM 633

Material

Fragment of theriodont maxilla together with a partial skull of the dicynodont Oudenodon in a large piece of matrix.

Locality

East London, Cape Province.

Collected

G. Mackay.

Original generic diagnosis

See holotype of Lycosuchus vanderrieti for generic diagnosis of Lycosuchus.

Original specific diagnosis

'L. mackayi is an animal at least a half larger than L. vanderrieti, ...' (Broom 1903d: 154).

References

Broom 1903d: 154, pl. XVIII Fig. 10

Haughton 1924: 76, 101

Broom 1932: 50, Fig. 16E

Kuhn 1937a: 118

Haughton & Brink 1955: 135

Kuhn 1965: 102

Kitching 1977: 53

Van den Heever 1980: 115,116.

Comments (Fig. 58)

Broom (1903d) established this taxon on the basis that the specimen was larger than L. vanderrieti. He was also of the opinion that the type of L. mackayi is represented by an immature individual. This assumption was probably reached because of the immature state of the posterior canine. If the specimen is assumed to be an early therocephalian the conditions of the canines reflect the usual replacement cycle. Because of the serrations, both on the front and the back of the teeth, the specimen is either an early therocephalian or a gorgonopsian. The single upper postcanine is of no real taxonomic value since the specimen is of such a fragmentary nature that the original number of postcanines cannot be determined. It is therefore impossible even to determine with certainty the infra-order to which the specimen belongs.

The same piece of matrix also contains a partial skull of the dicynodont Oudenodon. According to Cluver (pers. comm.) Oudenodon does not occur in the Tapinocephalus Zone. It is highly likely therefore that L. mackayi comes from the Cistecephalus Zone and in view of the paucity, if not complete absence of the early Therocephalia from this zone, the specimen is in all probability a gorgonopsian.

Haughton (1924) regarded it as a pristerognathid and stated the horizon to be Endothiodon Zone. Broom (1932) recorded only that he believed the horizon to be probably

higher than that of L. vanderrieti (Lycosaurus mackayi at his p. 50 is an error and should read Lycosuchus mackayi). Haughton & Brink (1955) referred the specimen to the family Lycosuchidae and gave the horizon as Endothiodon Zone. Boonstra (1969b) in his review of the Tapinocephalus Zone fauna consequently did not mention the specimen. According to Kitching (1977) L. mackayi is from the Cistecephalus Zone (sensu Kitching, 1972) and he correctly placed the specimen as Theriodontia incertae sedis. In view of the almost complete lack of diagnostic features Lycosuchus mackayi is here regarded as a nomen dubium.

Lycosuchus vanderrieti Broom, 1903

Holotype

US D173

Material

Nearly complete and least distorted skull of a lycosuchid therocephalian known at present; lacking right temporal arch, a portion of the left temporal arch, most of the right suspensorium, most of the left angular, the left septomaxilla, anterior extremities of the nasals, nasal processes of the premaxillae and the anterior portion of the right septomaxilla.

Locality

Groot Vlakte between Prince Albert, Beaufort West and Willowmore (see comments).

Collected

Presented by Rev. Van der Merwe.

Original generic diagnosis

The skull which is long and comparatively narrow, bears some superficial resemblance to that of Cynognathus platyceps, Seeley, but differs greatly in the structure of the lower jaw, and of the temporal arch, and in the dentition (p. 197). The maxilla is divided into a large upper portion and a small lower portion by a longitudinal ridge (p. 198). Differs from Ictidosuchus in that the jugal forms the lower half of the postorbital arch (p. 203) (after Broom 1903a).

Original specific diagnosis

As for genus.

References

Broom 1903a: 197-205

Broom 1903d: 154

Broom 1904b: Fig. 100A

Broom 1905b: Fig. 20A

Broom 1907c: 1053, Fig. 244D

Broom 1907d: Fig. 4A

Broom 1909c: Fig. 20

Broom 1910: 207,208

Zittel 1911: Fig. 329A

Nopcsa 1923: 122

Haughton 1924: 77

Williston 1925: 243

Broom 1932: 47,50, Figs 15B, 16B

Kuhn 1937a: 118

Romer 1945: 602

Gregory 1920: 134

Boonstra 1948: 43,47.

Gregory 1948: Fig. 5

Moret 1948: 575, Fig. 212E

Du Toit 1954: Fig. 48

Haughton and Brink 1955: 135

Romer 1956: Figs 96C, 102A

Von Huene 1956: 316

Watson and Romer 1956: 69

Lehman 1961: 233

Vjuschkov 1964: 277

Kuhn 1965: 102

Romer 1966: 373

Müller 1968: Fig. 626a,b

Kitching 1977: 36

Van den Heever 1980: 111-125

Comments (Fig. 59a-f)

In the type description of Lycosuchus vanderrieti Broom

(1903a) gave the locality as the Groot Vlakte, an area bounded by the towns of Pince Albert, Beaufort West and Willowmore. Later, (Broom 1903d p. 154) he noted that the specimen came from Karoo beds lying east of Beaufort West. Kitching (1977) recorded the locality as Fraserburg Road (now Leeu Gamka Station) Prince Albert, south-west of Beaufort West.

Broom (1903a) did not give a precise diagnosis of Lycosuchus vanderrieti but his description, which is largely correct, reflects the generalised early therocephalian features of this specimen. All that will be done here is to correct a few minor points and extend his description, especially with reference to the morphology of the palate, occiput and sidewall of the braincase which are now, as the result of additional preparation, visible for the first time.

There are 5, serrated, upper incisors in the right premaxilla of which the third tooth is being replaced. The left premaxilla contains 3 incisors with diastemas for two additional teeth in the first and third positions. In both maxillae the functional canines are being replaced. See Van den Heever (1980) for a discussion on tooth replacement in Lycosuch vanderrieti. Contrary to the observation of Broom (1903a) there are not one but three postcanines in the left maxilla. The hindmost tooth shows evidence of a serrated posterior edge. In the right maxilla two postcanines are present, the posterior one as a root only.

Broom (1903a) misidentified the septomaxilla as a posterior process of the premaxilla and, because the frontal

partially obscures the dorsal surface of the postfrontal he identified the postorbital as the postfrontal. Later (Broom 1932, Fig. 15B) he corrected these errors. Additional preparation of the inner roof of the orbit has revealed the postfrontal and postorbital in the usual configuration. Contrary to Broom (1903a) the nasals of Lycosuchus vanderrieti are not fused anteriorly, nor can the absence of an infraorbital foramen be regarded as positive evidence that the snout was covered with a horny plate. The orbits are located with their forward margins just anterior to the transverse midline of the skull.

The maxilla is similar to that of Hyaenasuchus whaitsi and Zinnosaurus paucidens in that is possesses a ventral maxillary flange on which the postcanines are implanted (Fig. 59c). In Lycosuchus, as in Hyaenasuchus, this portion of the maxilla lies more inward and is separated from the rest of the maxilla by a longitudinal ridge, the lateral maxillary ridge, extending from the canine region to below the orbit where it becomes confluent with the ventral margin of the jugal (Fig. 59c).

In Zinnosaurus the maxillary ridge is absent and the lateral surface of the ventral maxillary flange is confluent with the rest of the maxillary surface. In addition, the surface rugosities of the snout are also present on the ventral maxillary flange in Zinnosaurus, as opposed to the condition in Lycosuchus where the lateral surface of the ventral maxillary flange lacks rugosities and consequently

appears much smoother. Broom (1903a) held the view that in Lycosuchus this structure supported a fleshy lip which was attached to the lateral maxillary flange below the horny plate which, according to him, supposedly covered the rest of the maxilla.

The hardness of the matrix has generally impeded preparation but most of the palate, the right side of the occiput and the right side of the braincase are now revealed. The lower jaw is still in position as its removal will cause extensive damage to the specimen. A detailed description of the internal choanae and the anterior portions of the vomers is therefore not possible, but the posterior margins of the choanae can be seen to lie at a point in line with the posterior margin of the hindmost canine alvelous. The vomers do not form a ventromedial crest as in Pristerognathus but the usual expanded footplate of the bone contacts the anterior extremity of the pterygoid in the ventral midline of the palate. A suborbital fenestra is present and the pterygopalatine ridge terminates posteriorly in a small toothless boss.

The interpterygoid vacuity is wide and flanked by the posteromedial extremities of the transverse processes of the pterygoid as in Lycosuchus vanderrieti GS M793 and quite unlike the slitlike interpterygoid vacuity generally found in members of the Scylacosauridae.

The transverse process of the pterygoid has a sharp ventral margin. In the left process the remains of at least 3

but possibly 4 small teeth can be seen whilst on the right only one tooth is visible. The teeth are not implanted on the ventral margin of the transverse process but rather in a semilunate ridge on the anterior face of the transverse process (Fig. 59b). The quadrate ramus of the pterygoid terminates posteriorly between the quadrate head of the paroccipital process. It is not clear if the contact also includes a portion of the descending process of the squamosal behind the quadrate. A parabasisphenoid keel is present between the interpterygoid vacuity and the large posterolaterally directed basal tubera. The right stapes is slightly displaced, but present as a dorsoventrally flattened, dumbbell shaped bone, lacking a stapedial foramen. The distal head bears a small posterior process.

The epipterygoid is a flat, upright bone with a broad base supported by the quadrate ramus of the pterygoid. In lateral view it has the usual configuration; narrow waisted, with a broad apex and base as in all early Therocephalia.

The anterodorsal process of the prootic contacts the epipterygoid postermedially. A large fossa of which at least part of the inner wall appears to be formed by the supraoccipital, is present above the prootic.

A posttemporal fenestra is present but there is no evidence of a pterygo-paroccipital foramen. In occipital view the deep supraoccipital fossa is flanked by the tabulars. The dorsal margin of the posttemporal fenestra appears to be formed by the tabular, supra-occipital and opisthotic in much

the same way as illustrated for Regisaurus by Mendrez (1972b). The paroccipital process is usual in that proximally it forms the ventral margin of the jugular foramen and distally the mastoid and quadrate processes. A posttemporal fossa is not present.

As pointed out by Broom (1903a) a pronounced vertical crest is present on the posterior surface ofthe squamosal. According to him the sulcus immediately lateral to the crest is similar to the external acoustic meatus found in marsupials like the Tasmanian wolf Thylacinus. It is also reminiscent of the more elaborate system present in cynodonts like Diademodon. Since the sulcus leads ventrally towards the distal end of the stapes it is a reasonable assumption to regard the structure as evidence for the existence of an external acoustic meatus.

The left quadrate is partially visible with a remnant of quadratojugal supported by the lateral process of the quadrate roller.

The dentary has a pronounced angle and the lateral surface of the coronoid process is concave anterposteriorly, presumably for the insertion of a lateral portion of the adductor musculature. The splendial is not small, as described by Broom (1903a), but rather a thin flat bone applied to the ventromedial surface of the dentary, extending from the ventral margin ofthe symphysis to a point at least level with the plane of the transverse process of the pterygoid. Both angulars are damaged but show the usual

pattern of ridges and depressions on the outer surface. A postdentary foramen is present.

Broom (1908b) regarded Trosuchus, Hyaenasuchus and Lycosuchus as a separate group characterised by having two large incisors. He did, however, not establish these taxa as a family, and it was Nopcsa (1923) who erected the family Lycosuchidae. Haughton (1924) still regarded Lycosuchus vanderrieti as a pristerognathid but Williston (1925) followed Nopcsa (1923). Subsequently some authors i.e. Romer (1945) and Von Huene (1956) followed Haughton (1924). Notwithstanding, most authors viz. Haughton and Brink (1955), Vjuschkov (1964), Kuhn (1965), Boonstra (1953a, 1969b, 1971, 1972), Mendrez (1972a), Tatarinov (1974) and Kitching (1977) recognised the family Lycosuchidae. Romer (1956) placed Lycosuchus in a new family, the Trochosuchidae, as did Watson and Romer (1956) and Lehman (1961). Romer (1966) changed the family name to Trochosauridae. See Van den Heever (1980) for discussion.

The number of incisors and nature of the palate indicate that the specimen belongs with the Lycosuchidae. The presence of a lateral maxillary ridge and a ventral maxillary flange is here regarded as diagnostic and since Lycosuchus vanderrieti was the first described specimen to possess these features the taxon is regarded as valid.

Lycosuchus vanderrieti Broom, 1903

Referred specimen

GS M793

Material

Badly weathered lycosuchid skull with good palate and anterior two thirds of both dentaries; lacking anterodorsal portion of snout, most of superficial bone layer of snout, complete right postorbital arch, right temporal arch, right squamosal, most of right half of occiput and jaw articulation on both sides.

Locality

Booiskraal, Beaufort West.

Collected

A. Chuma.

Comments (Figs 9, 26, 30, 32, 60a-g)

Because of damage, the number of incisors is indeterminate, but serrations are present on all teeth. The postcanine regions of both maxillae are damaged and the remains of only 2 teeth are present in the left maxilla on what appears to be a ventral maxillary flange. All that can

be determined of the postcanine region of the right maxilla is the presence of one postcanine with the damaged alveolus of a second tooth behind it.

The choanae are short and whilst the pterygoid bosses are toothless the roots of at least 5 teeth are present on each transverse process. The basal tubera are large and the skull base below the sella turcica is broad in ventral view.

This specimen is a lycosuchid and because of the apparent presence of a ventral maxillary flange it is here referred to Lycosuchus vanderrieti. A morphological description of the specimen has been incorporated in chapter 4.

Lycosuchus keyseri sp. nov.

Referred specimen

GS C60

Material

Well preserved but somewhat laterally crushed skull and lower jaw of a lycosuchid therocephalian lacking the anterodorsal portion of the snout, right postorbital arch, lower portion of the left postorbital arch, both temporal arches, squamosals, posterior portions of the parietals, dorsal portion of the occiput, both stapes and jaw articulations.

Locality

Tygerhoek, Fraserburg.

Collected

A. W. Keyser.

Comments (Figs 4, 5, 7, 61a-v)

GS C60 is an undescribed specimen and is rare in the sense that it is one of only two specimens of the early therocephalia in which it has been possible, with the exception of the braincase, to expose most of the internal anatomy of the skull.

Because of the excellent preservation of those skull elements that are present in the specimen as well as the large amount of clear detail that they show, a comparative discussion of the general morphology of the skull has been included in Chapter 4.

The premaxillae are damaged but it is evident that a maximum number of 5 incisors was present on each side. The specimen lacks precanines and in the postcanine region there are 3 teeth present in the right maxilla and 5 in the left.

There are three serrated incisors in each lower jaw ramus of which the anterior two is about equal in size and the third considerably smaller. The lower canine is large, serrated and single in both rami. There is no evidence of canine replacement.

Seven postcanine position are visible in the right mandibular ramus. Serrated postcanines are present in the anterior 4, and last but one positions. At position 5 the

crown of a tooth about the size of those at position 1 and 3 appears to have been broken off, and at position 7 the remains of a smaller root is visible.

Six serrated postcanines are visible in the left mandibular ramus with an empty alveolus behind the last tooth. Medial to the fifth postcanine the serrated tip of a replacement tooth is visible

In both lower jaw rami there is evidence of alternate waves of tooth replacement since the odd-numbered teeth are larger than the even-numbered ones. The overall size of the teeth appear to decrease towards the back of the tooth row, indicating that the replacement waves may have proceeded from the front of the jaw to the back.

A crista choanalis is absent and the internal choanae are short. The pterygoid bosses are toothless but a number of roots are present on the transverse processes. The basal tubera are large.

The above features indicate that the specimen is definitely a lycosuchid but it does not possess a ventral maxillary flange as in Lycosuchus vanderrieti. The absence of this flange is here regarded as diagnostic and the specimen is named Lycosuchus keyseri in honour of Dr A.W. Keyser of the Geological Survey in Pretoria, who collected the specimen.

Mirotenthes digitipes Attridge, 1956

Holotype

UCMP 40467

Comments

This specimen consists of the skull and postcrania of a small therocephalian referred to the Pristerognathidae by Romer (1966). Miroteuthes at his p. 373 is an error and should read Mirotenthes. Attridge (1956) tentatively regarded the specimen as a whaitsiid in the type description and pointed out that none of the teeth were serrated. The specimen is consequently not an early therocephalian. Kitching (1977), who synonymised Mirotenthes digitipes with Ictidosuchoides longiceps of Broom (1920), stated that the specimen is from the Cistecephalus zone. Miroteuthes digitipesat his p. 53 is an error and should read Mirotenthes digitipes. Hopson (pers. comm.) has referred Mirotenthes to Hofmeyria atavus and pointed out that the palatal teeth described in the specimen by Cys (1971) do not exist, but are artefacts of preparation.

Moschorhinus kitchingi Broom, 1920

Holotype

BMNH R5698

Comments

Included by Haughton (1924) within the Pristerognathidae. It is evident, however, that the specimen is not an early therocephalian but an akidnognathid (sensu Hopson and Barghusen 1986) and is mentioned here only for the sake of completeness.

Moschorhinus warreni (Broom), 1907

Holotype

NM 188 (Type number 741).

Comments

Akidnognathid (sensu Hopson and Barghusen 1986) snout, incorrectly described as Scymnosaurus warreni by Broom (1907e) because the dentition appeared similar to that of Scymnosaurus ferox. Later (Broom 1932), he correctly referred the specimen to Moschorhinus and pointed out that it was found near the junction of the then Cistecephalus and Lystrosaurus Zones. Haughton and Brink (1955) reported the horizon as unknown.

Notaelurodon kitchingi Broom, 1936

Holotype

TM 272

Comments

Skull of a small therocephalian, thought by Broom (1936a) to be related to Hofmeyria atavus. Romer (1945) placed Notaelurodon in the Alopecopsidae together with, amongst other genera, Hofmeyria, but later (1956) doubtfully regarded it as a pristerognathid. Haughton & Brink (1955) included it within the Pristerognathidae whereas Watson & Romer (1956) placed it as Therocephalia incertae sedis. Von Huene (1956) retained Notaelurodon within the Alopecopsidae but Lehman (1961), Vjuschkov (1964), and Kuhn (1965) regarded Notaelurodon as a pristerognathid. Romer (1966) and Kitching (1977) doubtfully listed the specimen as belonging to the Pristerognathidae.

According to Hopson (pers. comm.) a minimum of 5 upper incisors are present in the specimen. It is clear, however, that on the basis of such features as the absence of tooth serrations and the presence of longitudinal ridges on the incisors and canines, Notaelurodon kitchingi definitely belongs with the later Therocephalia.

Pardosuchus whaitsi Broom, 1908

Holotype

SAM 1077

Material

Preorbital portion of a weathered scylacosaurid skull.

Locality

Near Fraserburg Road Station (now Leeu Gamka Station), Prince Albert.

Collected

J.H. Whaits.

Original generic diagnosis

Snout rather short; considerably broader in the canine region than immediately behind it; incisor region broad and rounded; jugals pass markedly outward at orbital region; incisor teeth unusually small and fairly round on section; posteriorly small serrated edge on incisors; first four teeth subequal (20mm); fifth incisor smaller and sixth very small; septomaxillary apparently forms whole of outer border of nostril and sends a process inwards a little below the middle of the opening; maxilla has two canines of which the anterior one is very small; large canine 11mm in anteroposterior diameter and about 38mm in height with a serrated posterior edge; five small molars (23mm); molars oval in section and show no serrations though no crowns are well preserved (after Broom 1908a: 367).

Original specific diagnosis

As for genus.

References

Broom 1908a: 367

Haughton 1924: 77

Williston 1925: 243

Broom 1932: 65,21D

Kuhn 1937a: 125

Von Huene 1938: 310

Romer 1945: 602

Haughton & Brink 1955: 127,139-140

Romer 1956: 697

Von Huene 1956: 317

Watson & Romer 1956: 69,88

Vjuschkov 1964: 277

Kuhn 1965: 96

Romer 1966: 373

Boonstra 1969b: 53,57,61

Tatarinov 1974: 105

Kitching 1977: 36

Comments (Fig. 62a-d)

The specimen is very poor and shows mainly detail about the dentition. Contrary to the description of Broom (1908a), the features regarded by him as diagnostic can, for most part, be attributed to distortion or to the condition found generally in scylacosaurids. The skull appears to be that of a subadult and as such explains the apparently short snout and relatively small teeth. The splayed condition of the jugals is most

certainly related to the dorso-ventral compression in the frontal area. The septomaxilla is identical to that of other therocephalians.

Additional preparation has shown the presence of 5 postcanines in the left maxilla and 3 in the right. Contrary to Broom (1908a) the first two on the left show serrations. The total number of postcanines are indeterminate and the fifth tooth may have been a replacement for the fourth. The morphology of the incisors and canines are not unique in any way.

As the result of the fragmentary nature of the specimen the vomers are visible in cross section at the level of the upper canines. Dorsally the vomerine keel is Y-shaped and ventrally a trough is present on each side at its base. The trough is formed by the upturned lateral edge of the bone. In cross section a distinct thickening, the crista choanalis, is visible on the maxilla, medial to the canines.

Anterior to the interpterygoid foramen the roots of at least 3 teeth are visible in a section through the left pterygoid boss. A portion of the ectopterygoid is visible at the lateral extremity of the transverse process of the pterygoid on each side.

The specimen possesses 6 serrated incisors as described originally. In addition, Broom (1932), in contrast to his previous description of Pardosuchus whaitsi (Broom, 1908a), pointed out the presence of two small precanines in the maxilla. Further investigation has shown that he was correct

and that these two minute teeth, which are present on both sides and were almost certainly non-functional, are indeed situated in the maxilla. Because of their poor condition it is not possible to determine if they were serrated or not.

Pardosuchus was originally placed in the Pristerognathidae by Haughton (1924) and in the Scylacosauridae by Williston (1925). Because of the presence of the two precanines Broom (1932) grouped the specimen with Alopecodon and Alopecideops in the new family Alopecodontidae. In contrast Von Huene (1938) and Romer (1945) placed it in the Alopecopsidae. Haughton and Brink (1955) returned the specimen to the Alopecodontidae whereas Von Huene (1956) placed it as Alopecopsidae and Romer (1956) in the Pristerognathidae. Watson and Romer (1956) and Kuhn (1965) referred it to the Pristerognathidae as well. Vjuschkov (1964) retained the specimen in the Alopecodontidae as did Romer (1966), Boonstra (1969b) and Kitching (1977). Tatarinov (1974) placed Pardosuchus in the subfamily Alopecodontinae within the Scylacosauridae. The Scylacosauridae was, however, regarded by him (Tatarimov 1974) as a separate taxon from the Pristerognathidae.

The presence of serrated teeth and an angle on the dentary indicate that the specimen is an early therocephalian. The teeth on the pterygoid boss and a crista choanalis on the maxilla show that it is a scylacosaurid.

Because the number of incisors and precanines are here regarded as diagnostic and SAM 1077 was the first described

specimen with the combination of 6 incisors and two precanines, Pardosuchus whaitsi is regarded as a valid taxon.

Pristerognathoides minor (Haughton, 1918)

Holotype

SAM 3415

Material

Superficially weathered but fairly complete skull lacking both temporal arches and right articulation of the lower jaw as well as much of the right squamosal and the dorsal parts of the parietals and the left squamosal; two fragments of lower jaw belonging to a different specimen; nine additional fragments of which two fit the right jaw articulation; one fragment of probable dicynodont postorbital/jugal.

Locality

Klipbank, Beaufort West.

Collected

The Rev. J.H. Whaits.

Original generic diagnos

Haughton (1918) originally placed this specimen as *Alopecognathus minor*. See holotype of *A. angusticeps* for generic diagnosis of *Alopecognathus*.

First emended generic diagnosis

Medium sized pristerognathids with dental formula

I.6,C.1,Pc.5-6; incisors small to fairly strong with sixth incisor only slightly to much smaller than its predecessors; canine fairly long; postcanines small, weak and well spaced; skull of medium size (max. length 222-287mm); preorbital depression shallow to fairly shallow continuing as a groove in the direction of the canine; septomaxilla fairly small; frontals with fairly small entry into the orbital border; prefrontal large with well marked lateral and dorsal face; postfrontal moderately well developed; snout wider than high; snout broader over last postcanines than over canines; orbits in posterior half of skull or just entering anterior half; skull very low over postorbital bar; orbits high up in skull; sagittal crest high with sharp edge; quadrate fairly low down, but well above lower border of the dentary; temporal fossa fairly long and moderately wide; premaxilla weak; squamosal with lateral edge not everted; angle of dentary squarish with fairly deep concave posterior edge sweeping far posteriorly towards the coronoid process; dentary shallow behind lower canine (after Boonstra 1954a: 94-95).

Second emended generic diagnosis

Dental formula I.6,C.1,Pc.5-6; postcanines small, weak and well spaced; lateral edge of squamosal not everted (after Boonstra 1969b:52).

Original specific diagnosis

Skull has 4 molars instead of 6 as in holotype of A.

angusticeps; eyes placed further forward than in A. angusticepts; differences exist in the relative positions of the teeth (after Haughton 1918: 180).

First emended specific diagnosis

There are 4 postcanines; maximum skull length 240?mm.; preorbital depression deep with very definite and abrubt margins; postorbital large (after Boonstra 1954a: 95).

Second emended specific diagnosis

As for first emended specific diagnosis.

References

Haughton 1918: 180-183, Figs 46-47

Haughton 1924: 76,101

Broom 1932: 56, Figs 17B&C

Kuhn 1937a: 120

Parrington and Westoll 1940: 313, Fig. 3c

Boonstra 1954a: 94-97, Fig. 12

Haughton and Brink 1955: 132

Kitching 1977: 38

Comments (Fig. 63 a-f)

SAM 3415 is superficially weathered over the entire surface of the skull. Subsequent to the description of Boonstra (1954a) a large portion of the occiput and skull base has been removed from the specimen and of the fragments now associated

with it, only two can be refitted to the skull with confidence. Both Haughton (1918) and Boonstra (1954a) recorded the overall skull length as 240mm which, despite the damage to the occiput, appears to be correct.

Fragments of 6 serrated incisors are present in each premaxilla and both functional canines are situated in the anterior alveolus. A diastema is present both in front and behind each functional canine. A frontal section through the snout shows that behind each functional canine the root of a smaller fang is present in the posterior canine alveolus (Figs 63e, 63f). In both maxillae the anterior surfaces of these roots have been resorbed by the larger root of the functional canine, indicating that the smaller fangs were previously functional. This interpretation is further supported by the fact that the canine roots in the posterior alveolus lack crowns. A plug of cancellous bone is present at the alveolar margin of the posterior canine in both maxillae, indicating that the crown has been shed and the root is in the process of being resorbed from the gumline upwards.

In the left maxilla there are 4 postcanines and in the right 5, all well spaced. Haughton (1918) recorded 4 postcanines in each maxilla. Boonstra (1954a) found 3 postcanines in the left maxilla and 4 in the right, although he did mention a possible fifth tooth in the right maxilla. Haughton (1918) described the postcanines as flattened, but these teeth are morphologically so poor that they will not bear description.

The anterior portion of the snout is completely devoid of the

outer layer of bone with the result that the external nares appear to face upward. The statement of Boonstra (1954a) that the bulge of the maxilla above the canine is not rugosely pitted is therefore impossible to verify.

According to Boonstra (1954a) the septomaxilla has a fairly large facial exposure, a well developed intra nostril spur (medial process) and a fairly large maxillo-septomaxillary foramen. Because of severe weathering no nasal process is visible and the septomaxilla is present only as a flat wedge of bone between the nasal, maxilla and the premaxilla. The size of the maxillo-septomaxillary foramen is normal for the size of the skull.

Contrary to Boonstra (1954a) the maxilla is not unusually long and low with a long overlap on the premaxilla. The surface of the specimen is badly damaged, but it is still clear that posteriorly the postero-lateral process of the maxilla extends well into the plane of the orbit and that anteriorly the anterior margin of the maxilla extends to the level of the fourth incisor as in early therocephalians generally. Dorsally the frontals and the nasals, as well as the dorsal borders of the maxillae, have been badly weathered, giving the skull a flatter and lower appearance.

The orbits are situated with their anterior margins on the transverse midline of the skull, as illustrated by Boonstra (1954a, Fig. 12b). According to Haughton (1918) the orbits in SAM 3415 are placed further forward than in the holotype of Alopecognathus angusticeps AMNH 5559. By comparing the two

specimens directly it is clear that the position of the orbits are similar in both.

Boonstra's (1954a) description of the preorbital depression is incorrect. Most of the lacrimal has been destroyed by grinding, creating a hollow with an artificially sharp margin in the matrix. All that remains within the depression are fragments of the lacrimopalatine ridge situated diagonally on the medial surface of the lacrimal.

Contrary to Haughton (1918) the postorbital arch is not weak and the maxilla and nasal are not separated by the frontal but by the prefrontal. According to Boonstra (1954a) the postfrontal has a large entry into the orbital border. The frontal usually overlaps the postfrontal dorsally, limiting its visible contribution to the orbital margin. In this instance the frontal has been weathered away, exposing a larger portion of the postfrontal. It is clear though that, contrary to Boonstra (1954a), the frontal is not excluded from the dorsal margin of the orbit as he states on p. 97. His statement also contradicts his own diagnosis for the genus. The post-frontal extends posteriorly for a short distance separating the parietal and postorbital. It is not possible to determine the entry of the postorbital into the orbital border, as is evident from Boonstra (1954a, Fig. 12b).

The parietals and squamosals are badly damaged dorsally and a sagittal crest, almost certainly present originally, is now absent. The parietal foramen has been enlarged by weathering.

Boonstras (1954a) description of the palate is essentially

correct but as a result of the poor preservation, the anatomy is not distinct.

Both Haughton (1918) and Boonstra (1954a) record teeth on the pterygoid bosses although none are now visible. The internal choanae extend posteriorly to a point well behind the level of the posterior canine alveolus. The transverse processes of the pterygoids are devoid of teeth and from the illustrations of Haughton (1918) and those of Boonstra (1954a), as well as the remains of the skull base on the specimen, it is clear that the basal tubera are small. According to Haughton (1918) the chief feature of the palate is its great length as compared to its breadth. The long narrow palate is, however, representative of all Scylacosauridae.

Haughton (1918) and Boonstra (1954a) described and figured the occiput in some detail. It is clear that the specimen has been damaged subsequently because in its present condition much of the occiput is missing and does not match the description. Nothing can be said about the occipital condyle and the jugular foramen since it cannot be seen anymore. Haughton's (1918) description of the elements surrounding the posttemporal fenestra cannot be verified in the specimen anymore but agrees closely with the condition in the early Therocephalia. The occiptal sutures are indistinct and the extent of the supraoccipital, although uncertain, appears to form at least part of the upper proximal border of the posttemporal fenestra.

The lower jaw is poorly preserved but from the remaining

portions it is clear that an angle was once present on the dentary. The symphysis is loose and the mentum slopes posteroventrally as in all therocephalians. According to Haughton (1918) the splenial does not contribute to the symphysis. The area in question is, however, covered in matrix and the splenial is not visible. It is doubtful if the spenial can be successfully uncovered without damaging the specimen. As the splenial does extend into the ventral portion of the symphysis in all early Therocephalia where this area can be examined, there appears to be no valid reason why it should be otherwise in this specimen. A coronoid process is present on the dentary above the badly weathered postdentary bones. A section through the articulation on the right shows the quadrate foramen with the quadratojugal lying lateral to it.

Haughton (1918) also discussed some points of the therocephalian braincase based on SAM 3415 and SAM 4332. Since both these specimens are so incompletely preserved in comparison with material recently found, the general aspects of the braincase has been discussed in Chapter 4.

Broom (1932) referred Alopecognathus minor SAM 3415 and Pristerognathus vanwyki SAM 6533 to Pristerognathus minor. Previously, Broom (1929) had already used the name Pristerognathus minor Haughton for a therocephalian shoulder girdle not associated with the type. Kuhn (1937a) accepted the identification of Broom (1932) but Boonstra (1954a) did not, and regarded SAM 3415 as Alopecognathus minor Haughton

albeit he utilized the specimen to represent the genotype of a new genus, Pristerognathoides, a view he later retained (Boonstra, 1969b).

Boonstra (1954a) based the original generic diagnosis of Pristerognathoides on 4 partial skulls i.e. SAM 3415 (genotype) with SAM 4332, SAM 3435 and SAM 11891 as referred specimens. The diagnosis consisted mainly of generalised, non-diagnostic early therocephalian features and was later (Boonstra 1969b) predictably superseded by a much abbreviated version.

The diagnosis of Boonstra (1969b) was based on the nature and number of the teeth as well as the condition of the lateral edge of the squamosal which was interpreted as 'not everted'. It has already been shown earlier in this investigation that in Alopecognathus angusticeps AMNH 5559, the so-called 'everted lateral edge ofthe squamosal' was an artefact of distortion. The absence of this condition in any other specimen can therefore not be regarded as a diagnostic feature.

SAM 3415 is certainly a poorly preserved specimen but the length of the choanae and palate, the tooth pattern on the pterygoids as well as the small basal tubera indicate that it belongs with the Scylacosauridae.

The presence of 6 upper incisors and lack of precanines show that it may be referred to Glanosuchus macrops. Pristerognathoides minor is therefore a nomen dubium.

Pristerognathoides minor Boonstra, 1954a

Referred specimen

SAM 3435

Material

Weathered and compressed scylacosaurid snout and lower jaw together with possible postcranial fragments in matrix attached to lower jaw.

Locality

Jakkalsfontein, Prince Albert.

Collected

Presented by A. M. Rodgers.

References

Boonstra 1954a: 98, Fig. 14

Kitching 1977: 37

Comments

This specimen consists of a poorly preserved snout wit 6 incisors, a single functional canine and 6 postcanines in the left maxilla. In the right maxilla 5 postcanines are present. Serrations are visible on all teeth. According to Boonstra (1954a) the preorbital depression has an abrupt anterior border as in the type of *P. minor* SAM 3415. Once again,

however, it has been excavated by grinding to such a degree that the diagonal lacrimo-palatine ridge (lamina verticalis ossis palatini of Tatarinov, 1974) on the medial surface of the snout is exposed, creating an artificial hollow. On the left no such depression exists but rather a shallow groove leading towards the canine. The snout is, however, laterally compressed and badly distorted.

The symphysis is loose as in all therocephalians and the nasal process of the premaxilla extend to a point in line with the posterior margin of the external nasal opening. The dentary is shallow immediately behind the canine.

It thus appears that the specimen was largely referred to P. minor on the basis of an artificial condition. It is noteworthy that the condition of the preorbital depression in the type is also the result of overgrinding.

Because of the presence of 6 incisors and the absence of precanines SAM 3435 is referred to Glanosuch macrops.

Pristerognathoides minor (Haughton) 1918

Referred specimen

SAM 4332

Material

Badly weathered skull lacking dorsal portions of parietals as well as the left squamosal, most of the right squamosal and

the right jaw articulaiton.

Locality

Wilgerbosch, Prince Albert.

Collected

S. H. Haughton.

References

Haughton 1918: 212-214 Fig. 59

Boonstra 1954a: 97 Fig. 13

Kitching 1977: 46

Comments

Boonstra (1954a) referred SAM 4332 to Pristerognathoides minor. The specimen is extremely weathered on the outside and much fragmented. Three lower and six upper, serrated incisors are present. In each maxilla the functional canine is situated in the anterior alveolus with the partially resorbed root of a previously functional canine in the posterior alveolus. No precanines are visible. Contrary to Boonstra (1954a) there are 6 and not 5 postcanines in the left maxilla of which the first and last are serrated both fore and aft. The right maxilla is too damaged to permit any definite conclusion, but there appears to have been at least 6 postcanines. The preorbital depressions are slight and have been enhanced by grinding. A shallow extension of the

depression extends in the direction of the canine on each side of the snout.

Because the specimen possesses 6 upper incisors and lacks precanines it is here referred to Glanosuchus macrops.

Pristerognathoides minor (Haughton) 1918

Referred specimen

SAM 11891

Material

Partial, badly weathered therocephalian skull lacking right postorbital half as well as the dorsal and lateral extremities of the snout.

Locality

Lammerskraal, Prince Albert.

Collected

J. Pienaar and L. D. Boonstra.

References

Boonstra 1954a: 98-99, Fig. 15

Kitching 1977: 40.

Comments

According to Boonstra (1954a) the preorbital depression is fairly shallow. In this specimen it is virtually non-existent, but has been enhanced by grinding as has the groove leading towards the canine position. Contrary to Boonstra's (1954a) count of 6 postcanines in the right maxilla there are only 5, one of which is well enough preserved to show serrations. Approximately 16mm behind the fifth postcanine a sixth tooth is present which is not implanted in the maxilla but appears rather to be a mandibular postcanine. Between the fourth and fifth upper postcanine on the right a diastema of approximately 11mm is present which would have contained at the very least 1 additional tooth since the postcanines in the left maxilla appear to have been closely packed.

The premaxillae are incomplete and the original number of incisors are therefore indeterminate. On the right, 5 upper incisors are visible, and on the left 4. A diastema is present anterior to the functional canine in the right maxilla.

In the left maxilla the functional canine is situated in the anterior canine alveolus. The posterior alveolus contains a previously functional canine of which the partially resorbed root is visible at the alveolar margin. The right maxilla is damaged dorsolaterally, revealing the root tip of a large canine in the posterior alveolus. The crown of this tooth is lost but its position is indicated by a large diastema in the tooth row. Anterior to the diastema the crown of the still, relatively small, functional canine is present.

The rest of the specimen is so poor that it hardly merits description. The postorbital arch is damaged and it is impossible to determine the contribution of the postorbital to the posterior border of the orbit, or the suture between the postorbital and jugal.

A medial section through the braincase reveals the basisphenoid keel and the sutures between the basisphenoid and the pterygoid, and between the basisphenoid and the basioccipital.

Because of the poor condition of the specimen and the intractable matrix, the entire palate and skull base is inaccessible. Dorsally the parietal foramen is clearly visible behind the interdigitating suture between the parietals and frontals.

As SAM 11891 revelas no distinct diagnostic features it is here considered as Scylacosauridae *incertae sedis*.

Pristerognathoides parvus Boonstra, 1954

Holotype

SAM 3611

Material

Badly weathered anterior two thirds of a small scylacosaurid skull with the anterior portions of both lower jaw rami and

the postorbital portion of a dicynodont skull of comparable size.

Locality

Bloukrans, Prince Albert.

Collected

Presented by C. S. Scholtz.

Original generic diagnosis

See holotype of Pristerognathoides minor for generic diagnosis of Pristerognathoides.

Original specific diagnosis

Skull small, low and fairly narrow; 5 small, well spaced postcanines; incisors weak, with fifth incisor weaker than anterior ones and sixth very feeble; diastema between incisors and canine great (15mm); canine slender; prefrontal large; skull very low over postorbital arch (after Boonstra 1954a: 102).

References

Boonstra 1954a: 102-103, Fig. 20

Haughton and Brink 1955: 133

Kuhn 1965: 97

Boonstra 1969b: 57

Comments (Fig. 64a-d)

This specimen consists of three skull fragments. So much of the outer surface has been weathered away that the anterior portions of the maxillae and most of the prefrontals, nasals and septomaxillae are missing. However, where preserved, the outer surface of the maxilla is rugose.

An unusual feature of the specimen is the wide intertemporal region with no evidence of a sagittal crest. The median suture between the parietals is not clearly visible and what appears to be the suture is in actual fact a crack extending along the skull roof and passing to the right of the parietal foramen. Anterior to the parietal foramen the skull roof is as wide as the interorbital region (30mm) and posterior to the parietal foramen it measures 22,5mm at the narrowest point. In addition the usual transverse suture between the frontal and the parietal cannot be seen either. These features are unusual in any early therocephalian and upon closer examination the postorbital portion of the specimen has been identified as that of a dicynodont by Cluver (pers. comm.).

According to Boonstra (1954a) the skull is small, low and fairly narrow. Without the dicynodont postorbital portion the specimen is that of a therocephalian with serrated teeth. It is not much distorted except in the region below the right orbit where the contact between the maxilla and the jugal flares laterally, enhancing the depth of the preorbital depression. Contrary to Boonstra (1954a) the preorbital

depression is shallow as can be seen on the less distorted left side. Unfortunately the depth of the right preorbital depression has also been affected by grinding.

Four well spaced postcanines are present in the right maxilla, the anterior tooth situated directly behind the canine. In the left maxilla 5 postcanines are visible of which the hindmost 3 are closely packed. As the result of a crack behind the first postcanine the second tooth is seen in the process of erupting. A diastema of 5,7mm is present between the left canine and the first postcanine. An additional postcanine may have been present in this position. The original number of postcanines therefore seems to have been at least 5 but possibly 6.

The canines although damaged appear slender. Both canines are located in the posterior alveolus. The remains of the anterior canine alveolus is visible in the right maxilla. A small tooth is present immediately anteromedial to this alveolus. Because this tooth is not located in the position of either a precanine or an incisor it is most likely a replacement for the previously functional canine in the anterior alveolus. However canine replacements usually migrate into the alveolus from a position directly medial to the alveolus so that by the time the tooth appears below the gumline it is already centered within the alveolus. The tooth in question satisfies none of these requirments and its nature must therefore remain in question. On the left a fragment of tooth is situated in approximately the same position. No

association is visible with the anterior canine alveolus but the tooth lies close to the ventral margin of the premaxilla-maxilla contact. As the result of weathering it is not possible to determine with certainty whether it is an incisor or a precanine.

Five incisors are visible in the right premaxilla with a large diastema behind the fifth tooth which may have contained an additional tooth. In the left premaxilla 4 incisors are present with an even larger diastema behind the fourth tooth which may have contained two additional incisors. The incisors are badly damaged and appear slender but do not seem excessively small.

The prefrontal is usual in that its anterior border lies in a plane level with the last postcanine and not the third as recorded by Boonstra (1954a, Fig. 20b).

Because of its gracile appearance SAM 3611 is most likely a scylacosaurid but, as definite diagnostic features are lacking, it is here regarded only as Scylacosauridae *incertae sedis*. *Pristerognathoides parvus* is therefore a *nomen dubium*.

Pristerognathoides parvus (Boonstra) 1953

Referred specimen

SAM 11944

Material

Laterally crushed and badly weathered posterior two thirds of a relatively small scylacosaurid skull lacking most of the squamosals as well as portions of the occiput and jaw articulation.

Locality

Buffelsvlei, Beaufort West.

Collected

J. Marais.

Original generic diagnosis

This genus is characterised by the small size of the skull (probable maximum length 162mm); large orbits (34x26mm); narrow snout, squarish in cross section; dentary not extending far posteriorly (after Boonstra 1953c: 62).

Emended generic diagnosis

Small pristeroganthids with dental formula unknown but probably I.6?, C.1?, Pc.4?; skull very small ((max. length (as reconstructed) 162?mm.)); preorbital depression very deep with sharp rim; frontal with moderate entry into orbital border; postfrontal well developed, orbits large and just entering anterior half of skull, sagittal crest of parietals fairly low, but with sharp edge (after Boonstra 1954a: 104).

Original specific diagnosis

As for genus.

Emended specific diagnosis

As for genus.

References

Boonstra 1953c: 62

Boonstra 1954a: 104-105

Haughton and Brink 1955: 131

Romer 1956: 697

Von Huene 1956: 316

Watson and Romer 1956: 69,88

Lehman 1961: 229

Kuhn 1965: 96

Romer 1966: 373

Boonstra 1969b: 51

Tatarinov 1974: 118

Kitching 1977: 34

Comments (Fig. 65a-d)

Boonstra (1953c) described this specimen as Maraisaurus parvus but later, (1969b), referred it to Pristerognathoides. The relatively small size of the specimen (parietal foramen to anterior border of orbit 40mm) and the large orbit indicate that it is a juvenile. What remains of the snout and lower jaw rami have been severely compressed laterally so that, in ventral view, little more than the left half of the palate can

be seen. Because of this the snout looks narrow, and in cross section, squarish.

The exposed root of a single postcanine is visible in the left maxilla and what appears to be the remains of two postcanines are present in the right maxilla.

Contrary to Boonstra (1953c), who stated that the dentary does not extend far posteriorly, it can be seen that the angle of the dentary reaches its usual position below the orbit. His other observation that the dentary does not curve much in dorso-posterior direction along its posteroventral margin is meaningless as both dentaries are damaged in this area. Both coronoid processes are also damaged and do not extend above the temporal arch. On both sides the lateral surface of the postdentary bones are damaged but in spite of that, a slight embayment of the anterodorsal edge of the angular, indicating the position of the postdenatry foramen, is seen. The right angular is virtually stripped of the reflected lamina. The left angular is more complete and it is evident that, contrary to Boonstra (1953c, 1954a) the notch between the body of the angular and the reflected lamina lies immediately posterior to the dorsal angular ridge and not anterior to it. By comparison with other specimens it is evident that the configuration of the angular ridges and the relation between the body of the angular and the reflected lamina in this specimen is similar to the general pattern found in the early Therocephalia.

Boonstra's (1953c) description of the quadrate is

essentially correct. However, he describes a transverse posterior groove above the condyle which, according to him, receives the descending plate of the squamosal medially and the base of the quadratojugal laterally. This is incorrect since the descending plate of the squamosal fits into a broad dorsoventral depression on the posterodorsal surface of the quadrate and the base of the quadratojugal rests on the lateral process of the quadrate roller forming the lateral margin of the quadrate foramen.

In the same paper Boonstra identified a portion of the quadratojugal at the left articulation. The fragment is question is, however, part of the quadrate and is confluent with it. The lateral portions of both quadrate rollers are missing and there is no evidence of the presence of either a quadratojugal or a quadrate foramen.

The epipterygoid has been exposed on the left and shows the configuration usual for the early Therocephalia eg. a broadened base and apex, with a narrow waist. A pterygo-paroccipital foramen is also present.

The sharp dorsal edge of the prefrontal (Boonstra 1954a) is the result of compression. As the bone is damaged on both sides of the snout its margins are not clear, but it appears to have a larger lateral than dorsal face and not <u>vice versa</u> as noted by Boonstra (1954a). He also believed the postorbital to be small but, because the surface ofthe skull roof has been ground away, the original extent of this bone, as well as the sagittal crest, cannot be accurately

determined.

The fairly long and wide temporal fossa (Boonstra 1954a) is the result of lateral compression. Boonstra (1954a) described the frontal as long but as the anterior portion of the bone is not preserved this statement cannot be verified. In Fig. 21a he does however indicate the anterior border of the frontal in the same position as for most of the genera discussed in his 1954a paper. The entry of the frontal into the dorsal border of the orbits is usual for scylacosaurids.

On the left the region immediately in front of the orbit has been crushed inwards and a hollow has been ground out of the specimen in search of the preorbital depression. This has further damaged the bone, creating an artificial hollow. On the left there is an indication of a very slight depression.

Because this specimen is a therocephalian with an angle on the dentary it is either a lycosuchid or a scylacosaurid. The presence of palatal teeth on the pterygoid boss, the small basal tubera, the absence of teeth on the transverse process of the pterygoid and the presence of a pterygo-paroccipital foramen indicate that it belongs with the Scylacosauridae. As additional diagnostic features are lacking and the holotype, Pristerognathoides parvus, is a nomen dubium, SAM 11944 is here regarded as Scylacosauridae incertae sedis.

Pristerognathoides peyeri Broili & Schröder, 1936

Holotype

UM 1936 II 9

Material

Weathered and dorsoventrally compressed skull and lower jaw of a scylacosaurid therocephalian lacking most of the occiput, squamosals and the posterior portions of both lower jaw rami.

Locality

Kleinwaterval, Prince Albert.

Collected

G. Grossarth.

Original generic diagnosis

See holotype of *Pristerognathus polyodon* for original generic diagnosis of *Pristerognathus*.

Emended generic diagnosis

See holotype of *Pristerognathoides minor* for original generic diagnosis of *Pristerognathoides*.

Original specific diagnosis

Skull unusually slender; dorsal surface realtively flat; lateral skull surfaces more or less vertical; preorbital depression large; orbit longer than wide and located completely in posterior half of skull; external nares located at the tip of the snout, longer than wide; interorbital wide; constituent skull bones as in Pristerognathus; suborbital fenestrae between palatines, pterygoids, and ectopterygoids large; upper tooth formula I.6, C.1, Pc.?7; teeth serrated with canine serrations very fine; suture present between dentaries at symphysis; splenial forms part of symphysis (after Broili & Schröder 1936b: 299).

References

Broili & Schröder 1936b: 283-310, Figs 1-6.

Haughton & Brink 1955: 132.

Von Huene 1956: Fig. 362.

Kuhn 1965: 98.

Boonstra 1969b: 57.

Kitching 1977: 38.

Comments (Fig. 66a-c)

This specimen was not studied at first hand but evaluated by means of the original detailed description of Broili & Schröder (1936b), and an excellent set of annotated photographs of the specimen which belonged to the late Dr Christiane Mendrez-Carroll. Originally established as Pristerognathus peyeri by Broili and Schröder (1936b) the

specimen was referred to Pristerognathoides peyeri by Boonstra (1969).

The skull is badly weathered but well prepared. The teeth are serrated and it has 6 upper incisors, no precanines, and apparently 7 postcanines. Broili & Schröder (1936b) pointed out that, as a result of the break in this area of the skull, the original number of postcanines are uncertain, but they considered there to have been probably 7 teeth.

The specific diagnosis of Broili & Schröder (1936b) is based on artefacts of distortion and generalised early therocephalian and therocephalian features. Pristerognathoides peyeri is consequently a nomen dubium. However, because it has 6 upper incisors, and no precanines it is here referred to Glanosuchus macrops.

Pristerognathoides roggeveldensis Boonstra, 1954

Holotype

SAM 9356a

Material

A badly weathered and distorted scylacosaurid skull consisting of the preorbital portion with lower jaw and a separate postorbital portion lacking the skull roof, temporal arches and right jaw articulation.

Locality

Roggekloof, Sutherland.

Collected

A.R.E. Walker.

Original generic diagnosis

See holotype of Pristerognathus polyodon for generic diagnosis of Pristerognathus.

Original specific diagnosis

Dental formula I.6,C.1,Pc.5; maximum length of skull 255mm; snout long, broader than high (52:50mm); orbit in posterior half of skull; dentary with truncated, posteriorly directed coronoid process (after Boonstra, 1953c: 60).

Emended generic diagnosis

See Pristerognathoides minor for generic diagnosis of Pristerognathoides.

Emended specific diagnosis

Skull long and narrow; 5 weak, well spaced postcanines; incisors fairly strong with sixth only slightly smaller than fifth; orbit well in posterior half of skull; squamosal extending well forward on lateral face of parietal; prefrontal narrow (after Boonstra, 1954a: 99).

References

Boonstra 1953c: 60, fig. III

Boonstra 1954a: 99-100, Fig. 16

Haughton and Brink 1955: 132-133

Kuhn 1965: 97

Kitching 1977: 42

Comments (Fig. 67a-c)

This extremely poor specimen was first described by Boonstra (1953c) and provisionally grouped in the genus Pristerognathus. Boonstra (1954a) transferred it to the genus Pristerognathoides. The diagnosis of Boonstra (1953c) is based on generalised, early therocephalian features. According to him the coronoid process is truncated and directed posteriorly. Unfortunately that portion of the skull is now missing and his observations cannot be verified. From the illustration (Boonstra 1953c: 59) it is evident that the coronoid process is located in its usual position. That the process in this single specimen was truncated, especially in view of the poor preservation, does not appear plausible. Consequently this feature was omitted by Boonstra (1954a) in the emended diagnosis of this specimen. Unfortunately the emended diagnosis of Boonstra (1954a) cannot be utilized as a specific diagnosis since it only indicates that the specimen exhibits some features of the Scylacosauridae i.e. 6 upper incisors and a snout that appears gracile.

Contrary to Boonstra (1953c, 1954a) there are only four

postcanines in the left maxilla and not 5. Three postcanines are present in the right maxilla with a diastema between the first and second tooth. The original number of postcanines are, however, indeterminate.

Boonstra's descriptions and illustrations of the posterior portions of the lower jaw is usual for the early Therocephalia but cannot be verified because of the missing portion. The ususual dome, formed by the squamosal in the posterior portion of the temporal opening and described by Boonstra (1953c), is an artefact of distortion. The contact between the quadrate and the quadrate ramus of the pterygoid as described by Boonstra (1953c) cannot be seen on the specimen.

In lateral view the epipterygoid is visible as a flat bone, pinched in the middle and with a broadened base and apex.

Contrary to Boonstra (1954a) the maxilla is neither long nor high. The bone extends from approximately the fourth incisor to below the orbit and its dorsal border contacts the nasal very close to the apex of the snout as in early therocephalians generally and as is evident from Boonstra's (1954a) own illustration of the specimen.

Because of weathering the configuration of the septomaxilla is indeterminate and the contribution of the frontals to the dorsal border of the orbit cannot be determined. The frontals are not preserved sufficiently to bear description and the postfrontals are missing. According to Boonstra (1953c) the width of the snout is 2mm more than the height. As a result of the severe compression of the skull it is impossible to

determine such small differences accurately. It is, however, true that in all early Therocephalia the snout is broader than high.

The outer surface of the preorbital portion is very badly weathered. On the left there is a slight indication of a preorbital depression, with what may have been a shallow groove leading towards the canine position. On the right the posteroventral portion of the maxilla flares laterally as the result of distortion, enhancing the right preorbital depression greatly.

According to Boonstra (1953c) the orbit lies in the posterior half of the skull and according to Boonstra (1954a) well into the posterior half of the skull. In view of the poor condition of the specimen the exact position of the orbit is difficult to determine but, compared with other specimens of equivalent size, it appears that the orbit lay with its anterior border on the midpoint of the skull as in all Scylacosauridae.

Boonstra (1954a) pointed out that the squamosal extends well forward on the lateral face of the parietal. The anteromedial margin of the squamosal is broken but a slight depression immediately anterior to the bone, indicates its original extent. This position lies just behind the plane of the angle between the parietals as in the early Therocephalia generally.

The configuration of the prefrontal cannot be determined in spite of Boonstra's (1954a) diagnosis that it is a narrow bone. In addition, Boonstra (1954a) described the lacrimal as

a large element and the orbit as small and situated high up in the skull. The poor condition of the specimen precludes any definite statements in this respect but, in spite of that, the position of the orbit and the size of the lacrimal appear normal.

This specimen is an early therocephalian because it possesses serrated teeth and an anteroposteriorly widened epipterygoid. Since no diagnostic features other than the presence of 6 upper incisors and a slender snout is present, Pristerognathoides roggeveldensis is regarded as a nomen dubium and referred to Glanosuchus macrops.

Pristerognathoides vanderbyli (Broom), 1925

Holotype

MM5139

Material

Weathered and partially distorted skull of a large scylacosaurid therocephalian lacking the dorsolateral portion of the right squamosal, most of both temporal arches and the postdentary bones of the right ramus of the lower jaw; portions of front limb and pectoral girdle are imbedded in matrix under the skull base.

Locality

Abrahamskraal, Prince Albert.

Collected

W.A. van der Byl.

Original generic diagnosis

See holotype of *Pristerognathus polyodon* for generic diagnosis of *Pristerognathus*.

Emended generic diagnosis

See holotype of *Pristerognathoides minor* for generic diagnosis of *Pristerognathoides*.

Original specific diagnois

Pristerognathus vanderbyli agrees very closely in size with *Pristerognathus polyodon* but is from a much lower horizon and may safely be regarded as a new species; premaxilla a little narrower and more pointed; symphysial portion of the lower jaw distinctly narrower; canines lie in true anteroposterior plane and not with posterior border directed considerably inwards (after Broom 1925: 317).

Emended specific diagnosis

As for original specific diagnosis.

References

Broom 1925: 316-318, one figure

Broom 1932: 55,56, Fig. 17A

Kuhn 1937a: 120

Haughton and Brink 1955: 132

Kuhn 1965: 98

Boonstra 1969b: 57

Kitching 1977: 32

Comments (Fig. 68a-d)

Although the skull is somewhat distorted, it is fairly complete. Broom (1925) referred the specimen to the genus Pristerognathus because it had 6 incisors and the lateral surface of the maxilla was rugosely pitted. Subsequently, however, the holotype of Pristerognathus polyodon was found to possess 7 upper incisors by Mendrez (1975a). In addition, all early Therocephalia have rugosely pitted maxillae. Broom (1932), in spite of the diagnosis given by him in 1925, pointed out that it was impossible to say in what way P. vanderbyli differed specifically from P. polyodon. He did however maintain P. vanderbyli as a discrete species because it came from a lower horizon.

Proximally the dorsal borders of the squamosals and the postero-lateral portions of the parietals have been deflected posteromedially, narrowing the angle between the parietals and causing the skull and the temporal fenestrae to appear longer. Broom's (1925) skull length of 287mm appears too ambitious and since the length from the tip of the snout to the anterior border of the orbit is 135mm the maximum length of the skull

is probably closer to 270mm.

The interorbital region has been depressed, damaging the dorsal borders of the orbits and causing them to appear elongate. Broom (1925) incorrectly regarded them as small and looking upward. They actually look outward and forward.

All the teeth are serrated and the incisors increase in size from the first to the fourth and then decrease progressively towards the sixth.

A slight step in the alveolar margin of the maxilla is present anterior to the left canine. This feature is not seen in the right maxilla. Both canines are large, lie in the anterior canine alveolus and are followed by a diastema. In both maxillae 6 well-spaced postcanines are present.

The external nares are damaged but the septomaxilla and the maxillo-septomaxillary foramen appear normal. Broom (1925) correctly illustrated the medial process of the septomaxilla but noted in the description that, unlike the gorgonopsians, P vanderbyli appears not to have possessed it.

The configuration of the snout bones is usual for early therocephalians and, contrary to Broom (1925), a postfrontal is present. A prominent sagittal crest is situated behind the parietal foramen. Unfortunately the occiput is completely covered with extremely hard matrix.

Much of the palate has been cleared. The pterygo-palatine ridges are devoid of teeth as are the transverse processes of the pterygoids. The roots of several small teeth are present on the pterygoid bosses. In the ventral midline, immediately

anterior to the interpterygoid vacuity a small distinct crest is present, as in the holotypes of Glanosuchus macrops and Alopecognathus angustioriceps. A similar structure is also found in the advanced Therocephalia (Eutherocephalia of Hopson and Barghusen, 1986). A parabasisphenoid keel is present and the basal tubera are small.

A shallow preobital depression which extends in the direction of the postcanines can be seen on the right. On the left this structure has been distorted as the result of dorsoventral crushing in the interorbital area.

Because the specimen possesses small basal tubera, teeth on the pterygoid bosses and lacks teeth on the transverse processes of the pterygoids, it is a member of the Scylacosauridae. The presence of 6 incisors, a ventromedial crest on the pterygoid and the absence of precanines show that MM 5139 may be referred to Glanosuchus macrops. Pristerognathoides vanderbyli is therefore a nomen dubium.

Pristerognathoides vanwyki (Broom), 1925

Holotype

SAM 6533

Material

Distorted and extensively weathered scylacosaurid skull lacking right postorbital arch, both temporal arches,

posterior portion of right jaw ramus and articulation; most of both squamosals as well as the lateral surface of the left jaw ramus.

Locality

Bloukrans, Prince Albert. (See comments.)

Collected

C. le Roux

Original generic diagnosis

See holotype of Pristerognathus polyodon for generic diagnosis of Pristerognathus.

Emended generic diagnosis

See holotype of Pristerognathus polyodon for generic diagnosis of Pristerognathoides.

Original specific diagnosis

The skull closely resembles that of Pristerognathus vanderbyli but is only about three quarters of the size; greatest length of skull about 220mm as compared with 287mm in Pristerognathus vanderbyli but molars occupy longer space by 2mm; distance from front of orbit to front of snout is 110mm as compared with 140mm in the larger species (after Broom 1925: 100).

Emended specific diagnosis

Skull moderately long and narrow; 6 weak well spaced post-canines; incisors fairly weak, with the sixth very slender; orbit just in posterior half of skull; prefrontal large; in lateral view maxilla short and high; septomaxilla has good facial exposure; orbit small and situated high up in skull; lacrimal large and preorbital depression shallow; skull fairly long and narrow in dorsal view; temporal fossa fairly short and narrow (after Boonstra 1954a: 100).

References

Broom 1925: 318-319

Broom 1932: 56

Broili and Schröder 1936a: 15

Boonstra 1954a: 100-102, Fig. 17

Haughton and Brink 1955: 133

Kitching 1977: 33

Comments (Fig. 69a-c)

According to Broom (1925) the locality of this specimen is Lammerkraal, Prince Albert but in the South African Museum catalogue the locality is recorded as Bloukrans, Prince Albert. The specimen is, however, extremely poor and exhibits no specifically diagnostic features.

Seven upper postcanines are present in the right maxilla as opposed to 6 mentioned by Broom (1925). Serrations are present on the better preserved teeth but the specimen is too

poor to determine the exact number of upper incisors. Three incisors are present in the right ramus of the lower jaw and both the left and right upper canine appears to be located in the anterior canine alveolus. Contrary to Broom (1925, 1932) a postorbital is present.

Broom (1932) synonymised Pristerognathus vanwyki with Pristerognathus minor (Haughton), both later included by Boonstra (1954a) in the genus Pristerognathoides. Broom (1932) regarded Pristerognathus vanderbyli as a separate taxon although he pointed out the possibility that P. minor might eventually prove to be the female or an immature specimen of the type of P. vanderbyli.

Boonstra (1954a) retained Pristerognathoides vanwyki as a separate taxon but his specific diagnosis of the specimen is based on generalised early therocephalian features.

Because of the poor state of the specimen no real diagnosis can be given at specific level. Pristerognathoides vanwyki is thus a nomen dubium but, because of the large number of upper postcanines, may be regarded as Scylacosauridae incertae sedis.

Pristerognathoides vanwyki (Broom), 1925

Referred specimen

SAM 11689

Material

Extremely badly weathered and dorsoventrally crushed skull of a scylacosaurid therocephalian, lacking most of the lower jaw and ventral surface of the skull.

Locality

Prince Albert Road (now Leeu Gamka), Prince Albert.

Collected

A.J. Hesse.

References

Boonstra 1954: 102, Fig. 19.

Comments

This specimen is in a very bad state of preservation. The nasal process of the premaxilla is long and extends to a point in line with the posterior border of the external naris. The dorsal surface of the skull is virtually stripped of bone. A shallow preorbital depression is present on the left. The right preorbital depression is more pronounced as the result of distortion and mechanical preparation.

The ventral surface of the palate is badly damaged and shows no diagnostic features other than the presence of suborbital fenestrae. Five serrated incisors are present in the right premaxilla with a large diastema between the fifth tooth and the canine. Four incisors are present in the left maxilla

with a large diastema between the first and second tooth as well as between the last incisor and the canine. The last tooth in the left premaxilla is small and may have been the sixth incisor. The possibility exists, however, that an additional incisor may have been present behind this tooth. The roots of at least 4 postcanines are present in the left ramus of the lower jaw. The number of upper postcanines is indeterminate.

Because of the generally poor condition of the specimen but especially the bad state of the teeth, SAM 11689 is regarded as taxonomically indeterminate. However, as it probably possessed at least 6 incisors, it is considered as Scylacosauridae *incertae sedis*.

Pristerognathoides vanwyki (Broom) 1925

Referred specimen

SAM 11893

Material

Very badly weathered and slightly distorted preorbital portion of a scylacosaurid snout and lower jaw.

Locality

Lammerkraal, Prince Albert.

Collected

J. Pienaar.

References

Boonstra 1954a; 100,102, Fig. 18

Kitching 1977: 40

Comments

A poorly preserved specimen which only exhibits general, early therocephalian features. According to Boonstra (1954a) only two postcanines are preserved in this specimen. In the left maxilla, however, at least 5 post-canines are visible of which the third tooth shows serrations. Six incisors are present of which the fourth is the largest and the sixth the smallest.

The sutures cannot be traced with accuracy and as the orbits are not preserved, the posterior extent of the maxilla cannot be determined. On the right the shallow preorbital depression has been enhanced by grinding. Immediately anterior to the right canine a step is present in the ventral border of the maxilla, a feature not present on the left maxilla. As the left maxilla is poorly preserved, the lack of this feature may be due to weathering. Both canines appear to lie in the anterior alveolus. No precanines are present.

This specimen is badly preserved but the large number of postcanines indicate that it belongs with the Scylacosauridae. Because it apparently possessed 6 upper incisors and no

precanines it is referred to Glanosuchus macrops.

Pristerognathus baini Broom, 1904

Holotype

SAM 583

Material

Weathered anterior extremity of snout and lower jaw of a small scylacosaurid therocephalian.

Locality

Western Karoo (Letjiesbosch, Beaufort West according to Kitching 1977: 40).

Collected

T. Bain.

Original generic diagnosis

See holotype of Pristerognathus polyodon for generic diagnosis of Pristerognathus.

Original specific diagnosis

Broom (1904a:87) failed to give a specific diagnosis of the specimen and only stated: 'It does not seem to present any character by which it can be distinguished generically from

Pristerognathus of Seeley, but it is a distinct species from P. polyodon Seeley. As in that species, so in this, the dental formula is I.6/3.

References

Broom 1904a: 87-88, Plate VI Figs 7-8

Broom 1908b: 370

Broom 1909a: 287

Broom 1913a: 363

Haughton 1924: 77,101

Broom 1925: 316

Broom 1932: 55, Fig. 17E

Broom 1936a: 355

Kuhn 1937a: 120

Boonstra 1954a: 86-87

Haughton & Brink 1955: 132

Kuhn 1965: 98

Boonstra 1969b: 51

Kitching 1977: 40

Comments (Fig. 70a-b)

Although not stated in the original description of the specimen by Broom (1904a), Pristerognathus baini was erected on its smaller size as compared with the type of P. polyodon BMNH R2581. Haughton (1924) pointed out that the specimen is probably unidentifiable because no postcanines can be seen. Broom (1932) mentioned that the two specimens probably belong

to the same genus but as species they are certainly distinct. He failed to say in what way he regarded P. baini specifically distinct from P. polyodon. Broom (1936) stated that the specimen was distinct and smaller. He also referred a skull with shoulder girdle and pelvis, collected at Letjiesbosch, Beaufort West, to Pristerognathus baini because it too was smaller than the type of P. polyodon.

Boonstra (1954a) listed the locality and the collector of the specimen as unknown and regarded P. baini as a junior synonym of P. polyodon (p. 86-87). Haughton and Brink (1955) recognised P. baini as a valid species. Later, Boonstra (1969b p. 51) stated that P. polyodon was a nomen dubium and that P. baini was therefore also a nomen dubium, based on the fact that 6 upper incisors occur in a number of therocephalian species and as a distinctive character it is not even of subordinal rank.

The specimen is badly weathered but can be recognised as a therocephalian because of the loose symphysis of the lower jaw. It is an early therocephalian because each ramus of the lower jaw has 3 incisors. There are 6 upper incisors, but this feature is not a distinctive character of Pristerognathus because Mendrez (1972a) shoed that the holotype of P. polyodon actually possessees 7 upper incisors in each premaxilla.

The lower incisors of P. baini is serrated. The lower half of each crown of the first incisor on both sides is serrated medially so that the cutting edges face each other. There is also a serrated edge on the posterolateral border of the first

incisor. The angle between the two rows of serrations is about 136 degrees and relates to the anteroposterior curvature of the alveolar border.

Because of distinct differences with the holotype of Pristerognathus polyodon, P. baini does not belong in this species. However, the presence of 6 upper incisors and the absence of precanines indicate that it may be referred to Glanosuchus macrops.

Pristerognathus polyodon Seeley, 1895

Holotype

BMNH R2581

Material

Extensively weathered scylacosaurid snout with anterior portions of both jaw rami. Septomaxilla, dorsal portions of premaxillae and anterior extremities of nasals missing.

Locality

De Cyfer, Tamboersfontein, Beaufort West.

Collected

H.G. Seeley.

Original generic diagnosis

The genus is defined by having the twelve incisor teeth in the upper jaw ovate in section, compressed from within outward; and the six incisor teeth in the mandible have the curved crowns compressed to sharp serrated edges, and decrease in size from the median line. The mandibular canines appear to be completely hidden when the jaw is closed (Seeley 1895: 997).

Original specific diagnosis

As for genus.

References

Seeley 1895: 994-997, Fig. 3

Broom 1904a: 87-88, Plate VI Fig. 7-8

Broom 1908b: 370

Broom 1909a: 287

Broom 1910: 198

Broom 1912: 864

Broom 1913a: 363

Haughton 1924: 77,101

Broom 1925: 316

Broom 1932: 53,55, Fig. 17F

Boonstra 1934: 217-218

Broom 1936a: 355

Kuhn 1937a: 120

Boonstra 1954a: 86,87

Haughton & Brink 1955: 131-132

Kuhn 1965: 97

Boonstra 1969b: 50-51

Mendrez 1972a: 2960-2961, one figure

Mendrez 1975a: 382,383-384, Figs 1-2, Plate 1

Mendrez 1975b: 18, Fig. A

Kitching 1977: 34

Comments (Fig. 71a-b)

When Seeley (1895) initially described Pristerognathus polyodon he was intrigued chiefly by the fact that each premaxilla possessed 6 incisors. This character has since remained the most prominent diagnostic feature of the genus. As early as 1932 Broom recognised that the specimen might be indeterminate because of its fragmentary nature. However, as other, similar specimens, had subsequently been found, i.e. P. baini, P. vanderbyli and P. minor, it was convenient to retain the taxon. Boonstra (1954a) believed the specimen to be of historic interest only. He proposed to retain the genus Pristerognathus for those therocephalian specimens possessing 6 upper incisors in a space of 35mm. Boonstra (1969b), however regarded Pristerognathus polyodon as a nomen dubium because, according to him, the presence of 6 upper incisors was not even a subordinal character and consequently, as a diagnostic feature, it had no value.

All other authors have consistently regarded the specimen as the valid genotype of the family Pristerognathidae, especially Mendrez (1972a) who, after additional preparation, established the presence of a crista choanalis, and correctly determined the number of upper incisors as 7. The crista is present as an inwardly projecting ridge on the medial surface of the maxillary canine boss and was interpreted by Mendrez (1972a) as the incipient development of a secondary palate. She therefore considered P. polyodon a valid taxon as did Kitching (1977) subsequently.

Pristerognathus polyodon BMNH R2581 has been described

and figured in detail by Mendrez (1975a) and need not be extensively discussed here.

Because it possesses 3 lower incisors, unfused vomers and serrated teeth, it is definitely an early therocephalian. Contrary to Mendrez (1972a, 1974) there is only one functional canine. The second alveolus is that of a previously functional canine which has been replaced. The presence of a crista choanalis and more than 5 upper incisors indicate that the specimen is a member of the Scylacosauridae. A total of 7 upper incisors and the complete absence of precanines is regarded as diagnostic.

As BMNH R2581 was the first specimen described bearing these features the name Pristerognathus polyodon is regarded as valid.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 631

Material

Badly weathered anterior extremity of a scylacosaurid snout without lower jaw.

Locality

Koup.

Collected

J.R. Joubert.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this speciment to the genus Pristerognathus. On the left there appears to be 7 incisors as in Pristerognathus polyodon BMNH R2581. On the right the remains of two canine roots are visible. Between the anterior tips of the nasals the nasal process of the premaxilla is visible. Both canines and incisors are serrated. On the left the broken crown of a single canine is visible.

Because this specimen has 7 incisors and no precanines it is here referred to Pristerognathus polyodon.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 751

Material

Badly weathered anterior extremity of a lycosuchid snout.

Locality

Seekoeigat, Prince Albert.

Collected

P.H. du Plessis.

References

Boonstra 1954a: 87.

Comments

This specimen was referred to Pristerognathus by Boonstra (1954a). It possesses three lower incisors and it is therefore an early therocephalian. Contrary to Boonstra (1954a) there are only 5 upper incisors and the specimen is therefore not Pristerognathus. An interesting feature is that the premaxilla and the vomer are exposed dorsally and the anterior extremity of the vomer is seen to overlap the premaxilla to such an extent that the dorsomedial lamina of the vomer extends to just behind the root postion of the first incisor.

Because of the presence of only 5 upper incisors SAM 751 is placed as Lycosuchidae incertae sedis.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 752

Material

Severely weathered piece of matrix showing faint markings of anterior extremity of possible therocephalian snout.

Locality

Seekoeigat, Prince Albert.

Collected

P. H. du Plessis.

References

Boonstra 1954a: 87.

Comments

This specimen was referred to Pristerognathus by Boonstra (1954a) but is so weathered that it is of no diagnostic value whatsoever.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 1075

Material

Very badly weathered anterior portion of a scylacosaurid snout.

Locality

Rietfontein, Prince Albert.

Collected

J. H. Whaits.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. There are three incisors in the lower jaw and it is therefore an early therocephalian. The upper incisors are, however, so badly damaged that only the remnants of three teeth can be seen in the left premaxilla. In posterior view the crista choanalis is clearly visible on the maxilla, medial to the lower part of the canine root on each side. Two postcanines are present in the right ramus of the lower jaw, the anterior of which is serrated both fore and aft. As the number of upper incisors are indeterminate and the specimen lacks all other diagnostic features except a crista choanalis, it is impossible to classify it below the level of family.

Therefore, because of the presence of a crista choanalis SAM 1075 is here regarded as Scylacosauridae incertae sedis.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 1213.

Material

Badly weathered dinocephalian jaw fragment showing the remains of 7 teeth.

Locality

Fraserburg Road.

Collected

J. H. Whaits.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus *Pristerognathus* but it is so badly preserved that it cannot be placed taxonomically with any certainty. It is not a scylacosaurid or a lycosuchid because it lacks the features diagnostic of these families. Also, the sheer size of the tooth that appears to be the canine, in relation to the other teeth, indicate that the specimen is of dinocephalian origin.

Boonstra (1954a) gave no record of the collector and listed the locality as unknown. In both instances however, the information is recorded in the South African Museum catalogue as supplied above.

This specimen is regarded as Dinocehpalia *incertae sedis*.

Pristerognathus sp. Seeley, 1895.

Referred specimen

SAM 3432

Material

Very badly weathered scylacosaurid snout with the anterior portion of the right lower jaw ramus.

Locality

Janwillemsfontein, Prince Albert.

Collected

S. H. Haughton & J. H. Whaits.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus

Pristerognathus. It is so badly damaged, however, that the median suture between the premaxilla cannot be observed. It is therefore not possible to determine with certainty the correct number of upper incisors but, judging by the relative sizes of the teeth, there were probably 6 in each premaxilla, as can be seen on the left. Only 5 incisors are visible on the right. The teeth are serrated and the first canine on the left has what appears to be a wear facet on its anterior surface. This feature is unusual in scylacosaurids since the teeth never occlude. Behind the canine root the roots of 3 postcanines are visible on each side.

The septomaxilla is well exposed showing the broad footplate anteriorly supported by the premaxilla. Posteriorly it extends as a pointed wedge between the nasal and the maxilla. All that is visible in the lower jaw is the root of a single canine.

The taxonomic position of this specimen is uncertain and since it appears to have had only 6 upper incisors it is not referable to Pristerognathus. It is therefore doubtfully placed as Glanosuchus macrops.

Pristerognatus sp. Seeley, 1895

Referred specimen

SAM 9015

Material

Badly weathered snout of a theriodont, missing the anterior portions of the premaxillae and the lower jaw.

Locality

Klein-Koedoeskop Beaufort West.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus but it is too badly weathered to determine the number of upper incisors. In the right premaxilla there are, however, the remains of two incisors and in the right maxilla, two postcanines of which the hindmost one is serrated both fore and aft. On the left a single postcanine is visible. The lower left canine is exposed and is shown to be extremely long. Although it is impossible to determine the specific status of this specimen, the lower jaw sumphysis appears loose as in therocephalians. However, both splenials are seen in ventral view and instead of being confluent with the ventral border of the dentary, as in therocephalians, they extend inwards to interrupt the otherwise smooth line of the ventral

aspect of the lower jaw, to form an angle of about 90 degrees with the symphysis, as in gorgonopsians.

Because of the damaged mentum there is no evidence of a true gorgonopsian chin and the apparent looseness of the symphysis may be the result of weathering. The exposed splenials and the angle they make with regard to the symphysis therefore indicate that this specimen is a gorgonopsian.

Pristerognathus sp.

Referred specimen

SAM 9084a

Material

Three weathered snouts of varying sizes, a left humerus of a gorgonopsian, and the centrum of a vertebra.

Locality

Rietkuil, Beaufort West.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred SAM 9084a to the genus Pristerognathus. Three snouts are included under this number, the smallest of which is that of a dicynodont (Cluver pers. comm.)

The second snout is misidentified since a break through the mentum shows that the specimen possesses 4 lower incisors. There are 5 upper incisors in each premaxilla and the third one on the left shows serrations along its posterior border. It is therefore a gorgonopsian.

The centrum of a vertebra with the same number is indeterminate, but may be that of a therocephalian. The humerus is gorgonopsian and has been figured by Boonstra (1965, Fig. 6).

The third snout with 3 lower incisors is that of a scylacosaurid. The specimen is considerably crushed dorsoventrally but seems to have possessed 6 upper incisors in each premaxilla. In the right maxilla the anterior canine is functional whilst the fang in the posterior alveolus is in the process of being resorbed from the gumline upwards. In the left maxilla a single large canine is visible. Anterior to each canine two precanines are present.

Four postcanines are visible in the left maxilla and 5 in the right. Lateral to the third postcanine on the right lies the remnant of a smaller, earlier tooth in that position. As a result of the fragmentary nature of the specimen the crown

of the first postcanine on the right is lost, but the whole root can be seen behind the second canine position. This root, like that of the canine immediately in front of it, is in the process of being invaded by cancellous bone from the gumline upwards. It appears that with the relative increase in size of successive canines in relation to skull growth, the most anterior of the postcanine postions may be invaded by the canine in the posterior alveolus because of spatial considerations. There is no evidence that the number of postcanines increase at the back of the tooth row. If the above is true, no diagnostic value at specific level can be attached to the precise number of postcanines in scylacosaurids.

Because of the presence of 6 upper incisors and 2 precanines this specimen is referred to Pardosuchus whaitsi.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 9111

Material

Weathered and laterally crushed snout and anterior portion of the lower jaw of a small scylacosaurid.

Locality

Die Vlei, Prince Albert.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

This specimen is an early therocephalian because it has 3 lower incisors in each dentary and the ventral border of the lower jaw is confluent with the symphysis. Six serrated upper incisors are present in each premaxilla with at least 5 postcanines in the left maxilla and at least 4 in the right maxilla.

An interesting feature of this specimen is that anterior to the single, large, serrated canine there are 2 small marginal precanines in each maxilla as in Pardosuchus whaitsi. In spite of being laterally compressed SAM 9111 does seem to have a more slender aspect than Pardosuchus whaitsi, but this condition may well be ontogenetic.

As no additional diagnostic features are present SAM 9111 is here referred to Pardosuchus whaitsi.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11456

Material

Weathered and slightly crushed snout of a scylacosaurid therocephalian.

Locality

Buffelsvlei, Beaufort West.

Collected

L. D. Boonstra & J. Marais.

References

Boonstra 1954a: 87.

Comments

Fairly well preserved snout with 6 incisors in each premaxilla. The ventral border of the lower jaw forms a straight line with the loose symphysis. The mentum is rounded and lacks the gorgonopsian chin. One canine is present in each maxilla. Two postcanines are present in the right maxilla and one in the left. Posteriorly, in each lower jaw ramus, one postcanine is seen in cross section.

Because of the number of incisors and lack of precanines this specimen is referred to Glanosuchus macrops.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11586

See *Cynariognathus paucioridens* referred specimen SAM 11586.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11842

Material

A badly weathered and crushed partial snout of a scylacosaurid.

Locality

Lammerkraal, Prince Albert.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. There are 3 lower incisors and the ventral border of the lower jaw is confluent with the symphysis. It is not possible to state with certainty whether there were 5 or 6 upper incisors present originally. In the right maxilla 5 postcanines are visible, but none in the left. Three serrated postcanines are present in the left dentary but none in the right. The upper and lower canines are single.

This specimen can only belong to either the Scylacosauridae or the Lycosuchidae and is therefore regarded as early Therocephalia incertae sedis.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11848

Material

Crushed and very badly weathered anterior extremity of a small therocephalian snout. Weathered centrum of indeterminate vertebra in matrix on left side.

Locality

Veldmansrivier, Prince Albert.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. The symphysis seems loose and together with the large number of incisors, the snout appears to be that of a scylacosaurid. The suture between the premaxillae is not clear because of crushing, but there appears to have been at least 7 incisors. The sepcimen is therefore most likely to be Pristerognathus polyodon.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11871

Material

Badly weathered anterior portion of a therocephalian snout.

Locality

Perdewater, Prince Albert.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. There are 6, serrated, upper incisors and the nasal processes of the premaxillae extend to a plane in line with the posterior borders of the external nasal openings. The nasals are expanded anteriorly and both the medial and posterior processes of the septomaxilla are distinct.

Because of the presence of 6 upper incisors this specimen is referred to Glanosuchus macrops.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11872

Material

Small piece of matrix with portions of premaxillae showing teeth.

Locality

Perdewater, Prince Albert.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. It consists of two partial premaxillae and in each bone there are 6 incisors. However, the nature of the specimen is so fragmentary that the original complement of teeth cannot be determined. The fact that it possessed at least 6 incisors in each premaxilla indicates that it is a scylacosaurid. It is therefore regarded as Scylacosauridae incertae sedis.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11873

Material

Extremely weathered anterior portion of a theriodont lower jaw with partial left maxilla and a portion of the palate.

Locality

Perdewater, Prince Albert.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristeroganthus. It is so badly weathered, however, that it is of no diagnostic value at all. The large number of serrated postcanines (at least 7) in the right ramus of the lower jaw indicate that it is a scylacosaurid. It is therefore regarded as Scylacosauridae Incertae sedis.

Pristeroganthus sp. Seeley, 1895

Referred specimen

SAM 11874

Material

Badly weathered and crushed, partial snout and anterior portion of lower jaw of a scylacosaurid.

Locality

Perdewater, Prince Albert.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. It has 6 serrated upper incisors in each premaxilla, no precanines, and a single large canine in each maxilla. Medial to the root of the right canine the maxilla shows a distinct crista choanalis. SAM 11874 is therefore referred to Glanosuchus macrops.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11875

Material

Badly weathered snout and anterior portion of the lower jaw of a theriodont.

Locality

Perdewater, Prince Albert.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. However, in ventral view, as in gorgonopsians, the splenials can be seen to project medially at the symphysis so that the symphysial line forms an angle of about 90 degrees with the ventral border of the lower jaw. Each premaxilla carries 5 incisors. A pterygo-palatine boss is present in the palate and small teeth are visible on this structure as in gorgonopsians. Although badly damaged the incisors appear to be unserrated, a feature not generally seen in gorgonopsians, but which apparently can be present in members of the Ictidorhinidae e.g.. Lemurosaurus (Sigogneau

1970: 342). There are also indications that one incisor possesses striations.

None of the above features tally with those seen in Scylacosaurids and the specimen is therefore regarded as a possible ictidorhinid.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11876

Material

Badly weathered preorbital portion of a therocephalian snout with anterior fragment of the lower jaw.

Locality

Perdewater, Prince Albert.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. It has the roots of 6 incisors in the right premaxilla, a single large canine and at least 3 postcanine teeth in the maxilla. The teeth are too damaged to show serrations and the mentum is too fragmentary to determine the number of lower incisors or the condtion of the symphysis.

The right maxilla overlaps the posterior portion of the premaxilla up to the level of the fourth incisor and the canines in the right maxilla show evidence of replacement. The large size of the specimen and the number of upper incisors exclude it as a possible member of the advanced Therocephalia or the Gorgonopsia, respectively. Because it lacks precanines it is referred to Glanosuchus macrops.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11936

Material

Fragmentary anterior portion of a theriodont snout without the left maxilla, nasals, lower jaw and most of the left premaxilla. The proximal and distal portions of a right femur is associated with the specimen.

Locality

Bosluiskraal, Laingsburg.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. Four robust incisor roots are visible in section in the right maxilla, with a space between the third and the fourth for an additional tooth. The canine is recognised by the greater size of its partial root as compared with that of the incisors. It is not possible to verify the existence of a crista choanalis, but the size of the snout together with its relatively low aspect indicates that it is probably an early therocephalian. Although it cannot be ascertained with certainty that the two portions of femur belong with the snout, the fact that they were given the same number originally probably indicates that they do. The two parts of the femur do however agree with the condition in scylacosaurids (Boonstra, 1964 Fig.6) rather than with that in gorgonopsians (Boonstra, 1965 Fig.7). Because the specimen appears to have possessed 5 upper incisors it is here regarded as Lycosuchidae incertae sedis.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11956

Material

Very badly weathered anterior extremity of a theriodont snout with the anterior portion of the lower jaw.

Locality

Klein-Koedoeskop, Beaufort West.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus but it is so badly weathered that almost all the diagnostic features are wanting. However, in ventral view the splenial forms an angle between the symphysis and the ventromedial border of the dentary as in gorgonopsians. The specimen is therefore not a therocephalian.

All the teeth are badly damaged and only the tips of some incisor crowns are partially preserved. No serrations are visible on these tooth fragments but what appear to be striations are present on the anterior surface of the undamaged tip of one incisor. Striated teeth are not diagnostic of the Gorgonopsidae but the configuration of the spenial as found in this specimen is. In view of the poor

condition of the teeth it would seem unwise to regard them as diagnostic but the possibility exists that SAM 11956 may be an ictidorhinid.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11957

Material

Weathered anterior portion of a snout and lower jaw of a scylacosaurid therocephalian; proximal extremity of a right femur associated with portions of the ischium and pubis forming the glenoid cavity.

Locality

Abrahamskraal, Prince Albert.

Collected

Presented by C. Le Roux.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus

Pristerognathus. It has the loose symphysis, sloping mentum and symphysial line confluent with the ventral border of the dentary as is usual in the Therocephalia. The 3 lower incisors and the serrations on the teeth show that the specimen is an early therocephalian. There are 6 upper incisors and although 1 upper postcanine is visible in the right maxilla the original number is indeterminate. A single large canine is visible in each maxilla anterior to which lies a single small marginal precanine as in Ictidosaurus angusticeps. The lateral surfaces of the maxillae are rugose as is usual in early therocephalians.

The head of the femur and associated pelvic fragment with the same number is that of a therocephalian but appear to have belonged to a somewhat larger animal. There is however no way of determining whether the cranial and pelvic portions definitely belong to the same animal.

Because of the presence of 6 incisors and 1 precanine the cranial portion is referred to Ictidosaurus angusticeps.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11960

Material

An extremely badly weathered scylacosaurid snout in three

pieces with anterior portion of the lower jaw.

Locality

Dikbome, Laingsburg.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. It has at least 6 upper incisors and shows a crista choanalis medial to the base of the upper canine root. It is, however, so badly weathered that no additional diagnostic features are readily apparent. Because of the large number of incisors and the presence of a crista choanalis it is here regarded as Scylacosauridae incertae sedis.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11963

Material

Weathered anterior portion of a scylacosaurid snout with anterior fragment of lower jaw.

Locality

Dikbome, Laingsburg.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. Six upper incisors are seen in each premaxilla with a crista choanalis present medial to the upper canine root on both maxillae. The symphysis is loose and 3 lower incisors are present in the right dentary. Because of the presence of 6 upper incisors and absence of precanines SAM 11963 is referred to Glanosuchus macrops.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11965

Material

Anterior extremity of theriodont snout with anterior fragment of lower jaw.

Locality

Skoppelmaaikraal, Laingsburg.

Collected

J. Botes.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. Four upper incisors are seen in the right premaxilla and two in the left. The total number of upper incisors are therefore indeterminate. The number of lower incisors can also not be determined because the portion of lower jaw is impacted into the anterior part of the palate. The nature of the symphysis and the mentum is indeterminate. As the result of weathering the existence of a crista choanalis cannot be verified with certainty. This specimen is therefore regarded as Theriodontia incertae sedis.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11966

Material

Weathered snout (Boonstra, 1954a).

Locality

Seekoeigat, Prince Albert.

Collected

T. Bain.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus but it now appears to be lost from the collections of the South African Museum.

Pristerognathus sp. Seeley, 1895

Referred specimen

SAM 11967

Material

Weathered anterior portion of a scylacosaurid snout with the anterodorsal portion of the lower jaw.

Locality

Seekoeigat, Prince Albert.

Collected

T. Bain.

References

Boonstra 1954a: 87.

Comments

Boonstra (1954a) referred this specimen to the genus Pristerognathus. The roots and partial crowns of 6 incisors are seen in the left premaxilla. In the right premaxilla 5 incisors are present with a diastema between the fourth and the fifth which probably housed another tooth. The posterior border of the root of the fourth incisor on the left appears to have slightly emarginated the anterior border of the fifth incisor. This is not a replacement phenomenon as the tooth replacing an upper incisor develops on its medial side.

The section through the mentum shows the right dentary with 3 incisors and a loose symphysis. Because the middle lower incisor is smaller than the other two teeth it is probably a

younger tooth. Medial to it lies a slightly larger tooth which is probably the replacement of the first incisor since the lower incisors are implanted at an angle. The anterior extremity of the left maxilla is damaged but overlaps the posterior portion of the premaxilla up to the level of the fourth incisor. Five postcanine roots are present in the right maxilla and six in the right dentary. The canine roots are large.

Because the specimen possesses 6 upper incisors and lacks precanines it is referred to Glanosuchus macrops.

Pristerosaurus microdon Boonstra, 1954

Holotype

SAM 9083

Material

Weathered and crushed scylacosaurid skull lacking precanine portion of the snout, left temporal arch, dorsal portions of the squamosals and parietals, distal portions of coronoid processes, and the right jaw articulation.

Locality

Rietkuil, Beaufort West.

Collected

L. D. Boonstra.

Original generic diagnosis

Fairly large pristerognathids with dental formula I.?, C.1, Pc.3 (in all probability there were 6 incisors); canine small and weak; postcanines also small, weak and closely packed; in all probability the incisors were also small and weak; skull fairly large (max. length 225 to 255?mm); preorbital hollow shallow to very shallow without definite margins; frontal with small entry into orbital border; postfrontal well developed; snout broader than high, not narrowed between orbit and canine; orbits in all probibility in anterior half of skull; sagittal crest of parietals high and sharp (after Boonstra 1954a: 82).

Original specific diagnosis

As for genus.

References

Boonstra 1954a: 82-83, Fig. 7

Haughton and Brink 1955: 133

Kuhn 1965: 98

Boonstra 1969b: 56

Kitching 1977: 42

Comments (Fig. 72a-b)

Boonstra (1954a) established the genus Pristerosaurus mainly

on the supposedly small upper teeth. However, both upper and lower incisors as well as the functional canines are missing. Most of the left maxilla is weathered away but the impressions of the two canine alveoli are visible in the matrix. The posterior alveolus is partially intact and contains a small replacing canine. The right maxilla is also damaged in the canine region but retains an area of cancellous bone high in the canine region such as that usually surrounding the canine roots in the early Therocephalia. This indicates that Pristerosaurus microdon possessed large canines. Further preparation of the left maxilla revealed an additional 3 postcanines so that the specimen possesses, contrary to Boonstra (1954a), not 3, but at least 6 upper postcanines. The postcanines are not unusually small, weak or closely packed as noted by Boonstra (1954a) as they are fairly well spaced and of the same size as that of Lycosuchus vanderrieti US D173, a skull of comparable overall size.

The preorbital depression is shallow and the entry of the frontal into the dorsal border of the orbit is usual. The fact that the snout is broader than high is a general feature of early therocephalians and not diagnostic at generic level.

According to Boonstra (1954a) the skull is not narrowed between the orbit and the canine. This feature cannot be determined because the area where the functional canines were situated is missing. Compared with a skull of similar size it is clear that the orbits lie in the posterior half of the skull with their anterior borders on the transverse midline as

in the Scylacosauridae.

According to Boonstra (1954a) the maxilla is short but high in lateral view. Unfortunately only the posterior and posteroventral portions of the right maxilla are reasonably well preserved and a definite statement about its configuration cannot be made.

The frontal appears usual in that its anterior extremity lies posterior to that of the prefrontal. The prefrontal lies in the usual position with exposure both on the dorsal and lateral surfaces of the snout. Anteriorly it terminates at a point in line with the position of the hindmost upper postcanine. The ridge on the prefrontal mentioned by Boonstra (1954a) is often seen in specimens and is enhanced by even slight distortion as in the type of Lycosuchus vanderrieti US D173.

Boonstra's (1954a) description of the jugal is correct except that it comprises only the lower part of the postorbital bar. The postorbital does not form the posterodorsal margin of the orbit, as noted by Boonstra (1954a), but the posterodorsal portion of the postorbital bar. As in all early Therocephalia the posterordorsal margin of the orbit is formed by the postfrontal.

The lower jaw is badly damaged and fragmented. The tooth bearing portions of both dentaries are missing and what remains of the right coronoid process lies outside the right temporal arch. The angle of the left dentary is visible, behind which portions of the angular and surangular are

present.

The temporal region is distorted with the result that the left temporal fenestra appears shortened and the right temporal fenestra appears lengthened. Notwithstanding, the temporal fenestrae do not seem exceptionally long or roomy. The parietal crest is high and sharp but the height may have been enhanced by distortion.

The occiput is damaged and the relationships of the constituent bones are consequently indistinct, but appears essentially as described by Boonstra (1954a) with the possible exception that the size of the posttemporal fenestra cannot be objectively assessed because of distortion. Contrary also to Boonstra (1954a) the basal tubera are not 'very strong' but lightly built as in the Scylacosauridae.

Haughton and Brink (1955) maintained P. microdon as diagnosed by Boonstra (1954a) and Boonstra (1969b) included the species in his subfamily Scymnosaurinae, as did Kitching (1977). None of the features regarded by Boonstra (1954a) as diagnostic are, however, valid and the specimen is here regarded as Scylacosauridae incertae sedis. Pristerosaurus microdon is therefore a nomen dubium.

Ptomalestes avidus Boonstra, 1954

Holotype

SAM 11942

Material

Badly weathered and dorsoventrally crushed scylacosaurid skull lacking left temporal arch, distal portion of the right postorbital arch, most of the left postorbital arch, dorsal and lateral portions of both squamosals, posterodorsal portions of both parietals, and most of the anterodorsal surface of the snout; with left and right radius and ulna, left humerus, distal portion of right humerus, a few cervical vertebrae, portions of the pectoral girdle, anterior two thirds of the left lower jaw ramus and complete right ramus of the lowe jaw.

Locality

Steenboksfontein, Laingsburg.

Collected

L. D. Boonstra.

Original generic diagnosis

Fairly large pristerognathids; dental formula I.5,C.1,Pc.6; incisors subequal and fairly weak; canine strong; postcanines small, slender and well spaced; skull fairly large (max. length 258mm); preorbital depression fairly deep but without abrupt margins and shallowing in the direction of the canine; frontal just entering orbital border; postfrontal quite well developed; snout broader than high,

only slightly narrowed between orbit and canine; orbits well in posterior half of the skull; mandibular symphysis formed solely by the dentaries, weak, unankylosed, mentum sloping; sagittal crest of parietals only moderately high and narrow (after Boonstra 1954a: 78-79).

Emended generic diagnosis

Five to six fairly weak postcanines (after Boonstra 1969b: 50).

Original specific diagnosis

In lateral view maxilla low, and long with long overlap on premaxilla; postcanines small, slender and irregularly spaced; maxillary edge curves upwards anterior to canine; 5 fairly small incisors, all more or less the same size; all teeth have serrated, sharp posterior edges (after Boonstra 1954a: 79).

Emended specific diagnosis

As for genus.

References

Boonstra 1954a: 78-81, Fig. 6

Haughton and Brink 1955: 131

Lehman 1961: 227, Figs 2D, 3A

Mendrez 1972a: 2961

Kitching 1977: 44

Comments (Figs 8,12,21,22,29,73a-h)

The skull of Ptomalestes avidus is badly crushed dorsoventrally and has previously, subsequent to the description of Boonstra (1954a), been subjected to acid preparation. The braincase and occiput were prepared completely but with some damage to the contacts between the bones and not all sutures can now be determined with certainty. Unfortunately the anterior part of the skull was not completely rid of acid at the time of preparation and has since deteriorated considerably. Rescue work done in 1970 by Mrs. I. Rudner, then employed by the South African Museum, has succeeded in stabilising the condition of the specimen. In certain areas, however, the bone had by this time been completely destroyed. Consequently the only remaining evidence of the original shape of the vomer is now preserved as a resin cast of the snout which was fortunately taken before the destructive action of the acid took effect. The condition of the anterior part of the skull is therefore such that most of the sutures cannot be determined with certainty.

Contrary to Boonstra (1954a) Ptomalestes avidus has 7 serrated upper incisors and not 5. In the right premaxilla only 5 incisors are visible with a diastema between the last and the canine, but in the left premaxilla there are seven teeth which increase in size from 1 to 4. The fifth is about the same size as the fourth with the sixth smaller and the seventh smallest. According to Boonstra (1954a) the incisors

are fairly weak. This is a subjective statement since the relative maturity of the teeth cannot be determined. Both functional canines are situated in the anterior canine alveolus. A distinct crista choanalis is present on the medial surface of the canine boss on each maxilla. Behind the left canine an area of cancellous bone indicates where a previous canine root was resorbed.

Five closely spaced postcanines are seen in the left maxilla. In the right maxilla 6 postcanines are present with spaces between the first and second, the third and fourth, and the fifth and sixth. The resin cast shows that no space originally existed between the third and fourth tooth. The plaster filled gap now present on the specimen is therefore most likely an artefact produced by acid deterioration. As the distance between the crowns of the functional canines differ by at least 20% in the cast and the specimen it is evident that some distortion has taken place. No remains of roots are visible in the spaces between the first and second, and fifth and sixth postcanines but it is possible that these gaps may have contained teeth. The possible number of postcanines are therefore taken to be 8. The right ramus of the lower jaw is well preserved and possesses 3 lower incisors, a single canine and 9 postcanines. Contrary to Boonstra (1954a) the splenial does contribute to the jaw symphysis.

The preorbital depression is distorted, but it is present as a shallow hollow extending in the direction of the canine.

Contrary to Boonstra (1954a) the lack of abrupt margins to the preorbital depression is not diagnostic. In Pristerognathoides minor SAM 3415, where this feature can be seen, it is shown to be an artefact of preparation. According to Boonstra (1954a) the frontal just enters the orbital border. This is incorrect as the right frontal clearly forms the dorsomedial portion of the orbital border between the prefrontal and the postfrontal as in most other Therocephalia. The postfrontal is situated between the frontal and the postorbital and extends posteriorly along the lateral surface of the parietal to at least the level of the parietal foramen. The postorbital lies lateral to and against the postfrontal forming the posteromedial portion of the postorbital arch.

The skull appears low because it is dorsoventrally compressed. In spite of this it is still apparent that the snout is broader than high and, in addition, narrowed between the canines and orbits as in all scylacosaurids. The size of the maxilla can still be determined, and in lateral view it extends dorsally to the apex of the snout in the canine region. From the poorly preserved sutures it can be seen to overlap the posterior portion of the premaxilla apparently up to the fourth incisor and terminate posteriorly below the orbit as in other scylacosaurids. Boonstra (1954a) incorrectly described the maxilla as long and low.

The orbits are situated with their anterior borders just behind the transverse midline of the skull. Taking into account the fact that a small portion of the skull roof is

missing at the fracture through the parietal foramen, the anterior border of the orbit was originally probably situated on the transverse midline of the skull.

The ventral border of the maxilla does have a step anterior to the canine as reported by Boonstra (1954a). This region is badly damaged and the feature can only be seen on the right side. Its presence is however not unique amongst early Therocephalia. The alveolar border of the upper jaw generally slopes upward from the postcanines in the direction of the incisors. Sometimes a slight step is present immediately anterior to the canine.

Externally the premaxillae are badly damaged and the condition of the septomaxillae, nasals and lacrimals is such that nothing can be determined about them.

A portion of the right temporal arch is present but does not readily fit on the skull. It does show however that the posterior process of the jugal extends posteriorly almost to the level of the quadrate as in Glanosuchus macrops GS M796. This process is dorsally overlapped by the anterolateral process of the squamosal to a point just behind the base of the dorsally directed postorbital process of the jugal.

According to Boonstra (1954a) the temporal fenestra is short but roomy. The shape of both fenestrae has clearly been influenced by dorsoventral compression, as well as a certain amount of shear. In spite of this the size of the temporal fenestrae does not appear unusual in any way. Within the temporal vacuity a pterygo-paroccipital foramen is formed by

outgrowths of the squamosal and prootic. Dorsally a sagittal crest is present.

The scylacosaurid palate is exemplified by the condition in Ptomalestes avidus. A ventral premaxillary foramen is present on the premaxillary table just behind the first incisor on each side. Anteriorly the vomerine processes of the premaxillae underlie the flat anterior portion of the vomers. The latter form a narrow inter-choanal bar and on the cast of the snout there is evidence of a ventromedial vomerine crest as in BMNH R2581 Pristerognathus polyodon.

Boonstra (1954a) described the paired internal choanae as short. However, they extend posteriorly well past the position of the posterior canine alveolus to a point level with the third upper postcanine. The choana is therefore as long as that of the scylacosaurid Glanosuchus macrops GS M796 as opposed to specimens with more robust skulls in which the posterior border of the internal choana does not extend beyond the posterior canine alveolus i.e. Lycosuchus vanderrieti.

A pterygopalatine ridge is present and it terminates posteriorly in a pterygoid boss containing the roots of a number of small teeth. The transverse processes of the pterygoids are devoid of teeth and between them a relatively narrow interpterygoid vacuity is present. As in all other scylacosaurids the basal tubera are small and the skull base below the sella turcica narrow.

All the features previously thought to distinguish Ptomalestes avidus have been shown to be either incorrect or

non-diagnostic. However, because the specimen possesses 7 upper incisors and lacks precanines, SAM 11942 is referred to Pristerognathus polyodon. Ptomalestes avidus is therefore here regarded as a synonym of P. polyodon.

Ptomalestes avidus Boonstra, 1954

Referred specimen

SAM 9012a

Material

Weathered anterior portion of a scylacosaurid snout (after Boonstra 1954a: 82).

Locality

Kleinkoedoeskop, Beaufort West.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 82

Kitching 1977: 38

Comments

According to Boonstra (1954a) the incisors of this specimen agree with those of the type. Unfortunately this specimen is now lost, but since it presumably did have 5 incisors it would not have agreed with the type which has subsequently been found to have 7 incisors.

Ptomalestes avidus Boonstra, 1954

Referred specimen

SAM 11460

Material

Badly weathered and dorsoventrally crushed scylacosaurid snout and lower jaw.

Locality

Buffelsvlei, Beaufort West.

Collected

L. D. Boonstra & J Marais.

References

Boonstra 1954a: 81

Kitching 1977:34

Comments

Additional preparation of this specimen showed that it possesses 6 incisors as opposed to Boonstra's (1954a) diagnosis of 5, no precanines and at least 5 postcanines. It is therefore referred to *Glanosuchus macrops*.

Scylacoides ferox Broom, 1915

Referred specimen

AMNH 5558

Material

Badly weathered and crushed gorgonopsian snout without lower jaw.

Locality

Beaufort West Commonage and surrounding flats.

Collected

Unknown.

Original generic diagnosis

It differs from *Aelurosaurus* in having 6 molars and in being much more heavily built; leangth of orbit to the tip of snout is about 102mm (after Broom 1915a: 119).

Original specific diagnosis

As for genus.

References

Broom 1915a: 119-120, Fig. 7

Haughton 1924: 77

Broom 1932: 57,68, Fig. 18G

Boonstra 1935a: 7

Kuhn 1937a: 122,127

Romer 1945: 602

Haughton & Brink 1955: 133

Romer 1956: 697

Von Huene 1956: 316

Watson & Romer 1956: 69,89

Lehman 1961: 231

Vjuschkov 1964: 276

Kuhn 1965: 99

Romer 1966: 373

Kitching 1977: 48

Comments (Fig. 74)

Broom (1915a) described and illustrated this specimen as a new genus and species of therocephalian. He noted that the specimen was so imperfect that any illustration of it would be misleading and that he was unable to definitely place the specimen either as a therocephalian or a gorgonopsian. The dental formula was recorded as I.5,C.1, Pc.6.

Haughton (1924) included the specimen in the Pristerognathidae. Broom (1932) again described and illustrated the specimen, stating on page 57, amongst the early Therocephalia, that it was difficult to determine if the specimen was a therocephalian or a gorgonopsian. On page 68 the same specimen is again included, presumably in error,

amongst the early Therocephalia.

Boonstra (1935a) found the tooth formula to be I.5,C.1,Pc.5 and stated clearly that it was not possible even to determine the suborder to which the specimen belonged.

In spite of Boonstra's (1935a) comments, Romer (1945: 602) included the specimen in the Pristerognathidae as did Haughton & Brink (1955), Romer (1956), Von Huene (1956), Watson & Romer (1956), Lehman (1961), Vjuschkov (1964), Kuhn (1965), and Romer (1966). Boonstra (1969b) did not mention the specimen and Kitching (1977) doubtfully included it within the Pristerognathidae, noting at the time that Boonstra (1935a) regarded it as gen. et sp. indet. Boonstra (1935a), however, stated clearly that the relevant suborder to which the specimen belonged was in doubt.

The specimen is badly preserved. The incisors and postcanines have been ground down and is present as root sections only. Each premaxilla has 5 incisors. In the right maxilla evidence of 5 postcanines are present. The left canine shows serrations and behind the right canine is an area of cancellous bone where a previous canine root has been resorbed. There appears to be no suborbital fenestra. The serrated teeth show that the specimen is either a scylacosaurid or a gorgonopsian and the apparent absence of a suborbital fenestra indicates thst it is most likely to be a gorgonopsian.

Scylacoides ferox is therefore placed as Gorgonopsia incertae sedis.

Scylacosaurus sclateri Broom, 1903

Holotype

SAM 634

Material

Weathered and slightly distorted skull of a small scylacosaurid therocephalian lacking the postorbital portion and the lower jaw.

Locality

Obtained at Colesberg, Cape Province.

Collected

Presented by D. Arnot.

Original generic diagnosis

Six incisors in each premaxilla, the last very small; minute first canine, large second canine and evidence of a third large immature canine; 7 small simple molars (after Broom, 1903c: 343-344).

Original specific diagnosis

As for genus.

References

Broom 1903b: 7

Broom 1903c: 343-345, Fig.

Broom 1903d: 147-151

Broom 1904a: 85,86

Broom 1907b: 159

Broom 1907c: 1048

Broom 1908a: 362,365,367

Broom 1908b: 370,371,372

Broom 1909a: 287

Broom 1910: 198,207,208,209, Figs 5,6

Broom 1913b: 226

Broom 1914: 16

Broom 1915a: 120

Haughton 1924: 78,101

Williston 1925: 243

Nopcsa 1928: 169

Broom 1932: 62

Boonstra 1934: 218

Kuhn 1937a: 123-124

Haughton and Brink 1955: 138

Kuhn 1965: 99

Kitching 1977: 50

Comments (Fig. 75a-d)

Broom (1903d) originally recorded the type locality of Scylacosaurus sclateri as Colesberg, Cape Province. This town

is situated in the Cistecephalus Zone and not the Tapinocephalus Zone, but no farm name is recorded and Broom (1903d) merely stated that the specimen 'was obtained at Colesberg' it may have been recovered from anywhere in the surrounding district or even farther afield, and brought to Colesberg. Since scylacosaurids and lycosuchids appear to be absent from the Cistecephalus Zone, the specimen was in all likelihood collected in Tapinocephalus Zone outcrops. In addition, Kitching (1977), has pointed out that the locality of Colesberg is unreliable.

Broom's (1903d) descriptive account of Scylacosaurus sclateri is predated by that of Broom (1903b), where the genus was named only and the Order Therocephalia established, as well as by Broom (1903c) where the taxon was diagnosed. The account of Broom (1903c) is therefore regarded as the original diagnosis.

Apart from certain features of the dentition the type of Scylacosaurus sclateri reflects the generalised scylacosaurid condition in the relationships of the constituent skull bones. The snout is long, narrow and pinched behind the canines. The interorbital width is narrow and the choanae long. The presence of a crista choanalis is indicated.

The skull is superficially weathered over its entire surface but a preorbital depression appears to have been present. Broom's (1903d) description of the snout bones is correct except that he regarded the septomaxilla as a process of the premaxilla and, in spite of the fact that the

premaxillae are largely weathered away anteriorly, described them as small.

The frontal forms the dorsomedial border of the orbit and both a postfrontal and a postorbital are present.

The palate is of the general scylacosaurid type. Anteriorly the premaxillae form the flat premaxillary table from which the vomerine processes extend posteriorly to underlie the anterior extremities of the vomers. The vomers are unfused, narrow and extend posteriorly as a narrow median girder separating the two long choanae which terminate posteriorly at the level of the posterior margin of the second upper postcanine. The remains of what appears to be a ventromedian crest is present on the vomers at the posterior margin of the choanae. Posteriorly the vomers expand to form a footplate which contacts the pterygoids in the ventral midline. This contact lies just behind the plane of the last postcanine as in lycosuchids. No teeth are present on the transverse processes of the pterygoids. Remnants of the pterygoid bosses and palatine ridges are present, flanked by the large suborbital fenestrae. What appears to be the roots of minute teeth are implanted on the pterygoid bosses only. The presence of a ventromedian crest on the pterygoid is indicated.

All the teeth are badly damaged and most are present as root fragments only. The absence or presence of serrations can therefore not be definitely established. Contrary to Broom (1903c,d) there are 7 and not 6 incisors in each

premaxilla. A single functional canine is present in the anterior alveolus in each maxilla with a diastema behind both. On the right the remains of the posterior canine alveolus is visible. It contained a canine only slightly smaller than the one in the anterior alveolus.

Immediately anterior to the functional canine a small marginal tooth is implanted in each maxilla. Because of the small size of these teeth they may not have protruded below the gum and were almost certainly non-functional. It also appears certain that they are not replacement canines because such teeth develop from a postion medial to the functional canine and then migrate laterally into the alveolus. By the time the tooth protrudes below the ventral margin of the maxilla the root extends well dorsally into the maxilla. None of the above applies to the small anterior canines and they are therefore interpreted as precanines. Seven upper postcanines are present in the right maxilla and 5 in the left. Because of the poor condition of the specimen it is not possible to determine if 7 was the full complement of upper postcanines.

Broom (1903b) regarded Scylacosaurus sclateri SAM 634 as the type genus of the Therocephalia and placed it in the family Scylacosauridae. Nopcsa (1923) recognised the family Scylacosauridae but Haughton (1924) placed Scylacosaurus sclateri in his new family the Pristerognathidae. Williston (1925) did not recognise the Pristerognathidae and retained Scylacosaurus in the Scylacosauridae as did Nopcsa (1928).

Broom (1932) erected a new family, the Ictidosauridae, to include Scylacosaurus, Ictidosaurus, Scylacorhinus and Akidnognathus. The Ictidosauridae was never recognised by any other author in this form as it included 3 'pristerognathids' and the advanced therocephalian Akidnognathus. Boonstra (1934), Kuhn (1937b), Boonstra (1938) and Von Huene (1938) placed Scylacosaurus in the Pristerognathidae. Camp and Vanderhoof (1940) recognised the Scylacosauridae but not the Pristerognathidae, whereas Camp, Taylor and Welles (1942) recognised both the Pristerognathidae and the Scylacosauridae. Romer (1954) recognised only the Pristerognathidae and included Scylacosaurus in the Alopecopsidae. Boonstra (1953a) placed Scylacosaurus in the Scylacosauridae but also recognised the Pristerognathidae. Haughton and Brink (1955) placed Scylacosaurus in the Akidnognathidae. Von Huene (1956) did not recognise the Scylacosauridae and placed Scylacosaurus in the Pristerognathidae as did Romer (1956), Watson and Romer (1956), Kuhn (1961) and Camp, Allison and Nichols (1964). Boonstra (1964) and Vjuschkov (1964) recognised both the Pristerognathidae and the Scylacosauridae. Kuhn (1965) and Romer (1966) recognised only the Pristerognathidae. Kalandadse et al (1968) and Tatarinov (1974) recognised both these families whilst Kithcing (1977) did not recognise the Scylacosauridae and returned Scylacosaurus to the Pristerognathidae.

On the whole the specimen is rather poor but the long snout and choanae, the large number of postcanines, the

presence of teeth on the pterygoid boss, a crista choanalis, and a vomerine process on the premaxilla show that it is undoubtedly a scylacosaurid. Since it is also the first named specimen to possess 7 upper incisors and 1 precanine the name Scylacosaurus sclateri is deemed valid.

Scylacosaurus sclateri (Broom), 1903

Referred specimen

AMNH 5560

Material

Very badly weathered palatal fragment of a scylacosaurid with anterior two thirds of lower jaw.

Locality

Near Beaufort-West.

Collected

J. H. Whaits.

Original generic diagnosis

The dental formula is I.7,C.2,M.8 and is practically intermediate between that of Alopecodon and Scylacosaurus (after Broom 1915a: 120).

Original specific diagnosis

As for genus.

References

Broom 1915a: 120-121, Fig. 8

Nopcsa 1923: 48

Haughton 1924: 78

Williston 1925: 243

Nopcsa 1928: 169

Broom 1932: 62,64, Fig. 21F

Zittel 1932: 262

Boonstra 1935a: 7-9, Fig. 3

Kuhn 1937: 124

Romer 1945: 602

Haughton and Brink 1955: 138

Romer 1956: 697

Von Huene 1956: 317

Watson and Romer 1956: 69

Lehman 1961: 230

Vjuschkov 1964: 276

Kuhn 1965: 99

Kitching 1977: 41

Comments (Fig. 76a-b)

This extremely poor specimen, initially described as Scylacorhinus falkenbachi by Broom (1915a), partially shows the dorsal surface of the palate and in lateral view, the

teeth. The sloping mentum, the loose symphysis and the serrated teeth indicate that it is an early therocepahlian.

In each premaxilla 7 incisors are present as in Pristerognathus. Anterior to the large canine in the left maxilla, a small marginal precanine is present. In dorsal view, the roots of two canines can be seen in the left maxilla. The anterior tooth is the largest and presumably the youngest, since a frontal section through the alveoli shows that it has partially invaded the anterior surface of the canine root behind it. There are no teeth on the transverse process of the pterygoid, but the roots of at least 2 teeth are visible on the pterygoid boss. The remains of 8 postcanines can be seen in the left maxilla. Broom (1932) incorrectly figured the specimen with 6 upper incisors and regarded it to possess 9 postcanines.

What can be seen of the dorsal surface of the palate, shows the suborbital fenestra formed by the palatine, ectopterygoid and pterygoid. The posterior margin of the choana is dorsally bordered by a ridge formed by the palatine. Behind the ridge is a depression which is posteriorly bounded by a second ridge extending anteromedially from the anterior border of the maxillary antrum to the midline. Boonstra (1935a) regarded these structures as a system of girders which served to strengthen the palate.

Subsequent to the description of Broom (1915a) this specimen has been regarded as a member of the Scylacosauridae by Nopcsa (1923, 1928), Williston (1925) and Vjuschkov (1964).

However, Haughton (1924), Boonstra (1935a), Romer (1945, 1956), Watson and Romer (1956), Lehman (1961), Kuhn (1965) and Kitching (1977) regarded it as a pristerognathid. Despite the fact that Boonstra (1935a) pointed out that the specimen could be referred to Scylacosaurus sclateri, Kuhn (1937, 1965), Romer (1956), Von Huene (1956), Watson and Romer (1956), Lehman (1961) and Vjuschkov (1964) still recognised Scylacorhinus as a separate taxon.

Consequently, because the specimen is in a very poor state and shows no diagnostic features other than the nature of the dentition, in which it agrees with that of Scylacosaurus sclateri in the number of incisors and precanines, Scylacorhinus falkenbachi is regarded as a junior synonymn, and in agreement with Boonstra (1935a) and Kitching (1977) specimen AMNH 5560 referred to Scylacosaurus sclateri.

Scylacosaurus sclateri Broom, 1903

Referred specimen

BMNH R4055

Material

Weathered and fragmentary skull of a small scylacosaurid.

Locality

Fraserburg Road Station, now Leeu Gamka.

Collected

J. H. Whaits.

References

Broom 1914: 30, Plate 4 Fig. 43

Boonstra 1934: 218-223, Figs 2-5

Boonstra 1935a: 8

Romer 1956: Fig. 98a

Müller 1968: Fig. 624a,b,c.

Comments

This specimen is badly preserved but possesses 8 upper teeth anterior to the canine as well as tooth serrations. Boonstra (1934) regarded the hindmost 3 of these teeth as precanines and numbers 1-5 as incisors. However, after studying the American specimen AMNH 5560 he (Boonstra 1935a) pointed out that it remained uncertain whether these teeth were incisors or precanines. Additional preparation of the teeth in question has now revealed the presence of what appears to be 7 upper incisors and 1 precanine. The precanine is larger than the last incisor.

Contrary to Boonstra (1934) the basisphenoid is not widened. The fenestra ovalis is visible but the area in question is so damaged that only the general relationships of the bones can be determined and their configuration agrees with the consdition found in scylacosaurids.

A pterygoid boss appears to be present but the bulge on the paroccipital mentioned by Boonstra (1934) cannot be verified. Contrary to Boonstra (1934) there are only 6 postcanines present in each maxilla. A diastema is, however, present in the left maxilla between the 4th and 5th postcanine and it may have contained an additional tooth.

This specimen is a scylacosaurid and on the available evidence is interpreted to possess 7 upper incisors and a single precanine. In accordance therefore with Boonstra (1934, 1935a) BMNH 4055 is retained as a referred specimen of Scylacosaurus sclateri.

Scymnosaurus ferox Broom, 1903

Holotype

SAM 632

Material

Anteroventral snout portion of a large lycosuchid with anterior extremities of both lower jaw rami.

Locality

Unknown.

Collected

Unknown.

Original generic diagnosis

With the exception of Titanosuchus this is the largest primitive theriodont known at present; 5 incisors, 1 canine and 3 molars with evidence of an additional canine lost; vomers very much broader than in Scylacosaurus, but only form a small part of hard palate (after broom 1903d: 152).

Emended generic diagnosis

Large pristerognathids with dental formula I.5,C.1,Pc.2-4; incisors and canines large and strong, postcanines fairly weak to medium, varying in number - 2,3 or 4. (In one specimen a small 6th incisor has been seen, but only on the one side). Skull very large (Max. length 375 to 475mm); preorbital hollow fairly shallow, not sharply demarcated and really not more than a groove stretching from the orbit in the direction of the canine; septomaxilla and septomaxillary foramen well developed; frontal either excluded or possibly just entering the supraorbital border; snout probably always slightly broader than high, slightly narrowed between orbits and canines; orbits partly in anterior half of skull; mandibular symphysis, formed solely by dentaries, weak, unankylosed, mentum sloping little or moderately (after Boonstra 1954a: 69).

Second emended generic diagnosis

Postcanines fairly weak to medium varying in number - 2, 3 or

4 (Boonstra 1969b: 50).

Original specific diagnosis

As for genus.

Emended specific diagnosis

There are 3 to 4 postcanines; mentum moderatley sloping and symphysis weak; maximum length of skull 375-381mm (as reconstructed); frontal possibly still entering orbital border (after Boonstra 1954a: 69).

Second emended diagnosis

As for genus.

References

Broom 1903d: 152-154, Fig. 6-9

Broom 1907e: 171

Haughton 1924: 78,101

Broom 1932: 59, Fig. 19D

Kuhn 1937a: 122

Romer 1945: 602

Boonstra 1954a: 69-70, Fig. 1a

Haughton and Brink 1955: 133-134

Kuhn 1965: 100

Kitching: 1977: 41

Comments (Fig. 77a-c)

This specimen is large and appears to approximate Scymnosaurus major SAM 9005 in size. It can be recognised as a therocephalian because the loose symphysis lacks a gorgonopsian chin and an anteriorly expanded splenial. The ventral border of the lower jaw consequently forms a straight line with symphysis. The presence of tooth serrations indicate that it is an early Therocephalian.

The diagnosis of Broom (1903d), which noted differences with other established species of that time, is not altogether correct because the specimen is broken off behind the third postcanine and the original number of postcanines is therefore indeterminate. It is also incorrect to say that the vomer is very much broader than in Scylacosaurus, because the latter is a much smaller specimen, in which the vomer can only be seen in ventral view. In Scymnosaurus ferox the vomer can only be seen in dorsal view and, owing to the oblique coronal fracture, the section is not horizontal. However, in direct measurement the width of the vomer in both skulls are approximately 25% of the width of the snout at the alveolar margin in the canine region. Broom (1932) reiterated that he regarded 3 postcanines to be the full complement.

Immediately anterior to the roots of the first, second and third incisors on the left are the partially resorbed remains of their predecessors. On each side the canine region shows evidence of tooth replacement. Behind both canines remnants of previously functional fangs are visible in the posterior alveolus. Because of the oblique coronal section,

extending downwards from left to right, only the root tip of the smaller, earlier canine in the left maxilla is visible. In the right maxilla, where the section is closer to the alveolar border, the earlier root is shown to be already partially resorbed. An interesting point is that the same canine root has partially resorbed the root of the first postcanine. It appears certain therefore that with consecutive increments in size, the canine in the posterior alveolus will progressively encroach upon the anterior postcanine postions. The number of postcanines is therefore not a valid diagnostic feature at species level.

Since 5 incisors are not diagnostic at generic level it would seem as if the sheer size of the specimen is its only distinguishing feature. The inexpedient use of skull size as a taxonomic feature in the early Therocephalia has already been discussed earlier.

Boonstra (1954a) referred three specimens (SAM 3430, SAM 4341, SAM 9084) to the genus Scymnosaurus. His emended diagnosis for the genus is however non-diagnostic because it is predominently based on generalised early therocephalian features. Contrary also to his statement that the mandibular symphysis is formed only by the dentaries, additional preparation has shown that the anterior extremity of the splenial does enter the symphysis as in all known early Therocephalia.

The frontal is not preserved in any specimen except SAM 9084 (referred to S. ferox) and SAM 9005 (Scymnosaurus major)

and in both specimens it forms the middle portion of the dorsal margin of the orbit as in all therocephalians. Boonstra (1969b) reduced the diagnosis of the genus Scymnosaurus solely to the number and nature ofthe postcanines.

Since SAM 632 is so fragmentary that it lacks all diagnostic features except 5 upper incisors it can only be placed as Lycosuchidae incertae sedis. Scymnosaurus ferox is therefore a nomen dubium.

Scymnosaurus ferox Broom, 1903

Referred specimen

SAM 3430

Material

Badly weathered preorbital portion of a large lycosuchid skull without frontals, nasals and dorsal portions of septomaxillae and premaxillae; anterior extremities of both lower jaw rami in position.

Locality

Jan Willemsfontein, Prince Albert.

Collected

S. H. Haughton and J. H. Whaits.

References

Boonstra 1954a: 70, Fig. 1b

Kitching 1977: 37

Comments

According to Boonstra (1954a) this specimen has 6 incisors on the left, the last being the stump of a small tooth. Preparation and staining of this region has revealed

that it is the remainder of a very large tooth and as its position in the left maxilla compares with that of the canine in the right maxilla it is most probably a fragment of an older canine in the anterior canine alveolus.

Boonstra (1954a) noted the presence of 4 postcanines in the right maxilla, the first and third represented by diastemas. The anterior diastema is however that of the posterior canine alveolus. There is consequently space for 3 postcanines only. Because of the fracture in the postcanine region it is possible that there may have been additional teeth.

As a result of the lack of diagnostic features this specimen is placed as Lycosuchidae *incertae sedis*.

Scymnosaurus ferox Broom, 1903

Referred specimen

SAM 4341

Material

Badly weathered anterior portion of the snout of a large scylacosaurid with the anterior extremities of both lower jaw rami.

Locality

Stinkfontein, Prince Albert.

Collected

S. H. Haughton.

References

Boonstra 1954a: 71, Fig. 1c

Kitching 1977: 44

Comments

This specimen is a generalised early therocephalian and Boonstra's (1954a) description is correct except for the number of incisors and postcanines. In each premaxilla there are 5 large incisors followed by a very small premaxillary tooth. Both these teeth lie close to the last incisors and in line with them as opposed to the marginal position of the precanines in other specimens viz. the holotype of Theriodes cyniscus SAM 11888. They are therefore regarded as incisors. There are 5 postcanines in the right maxilla. Both canine alveoli in the right maxilla are seen in dorsal view with the functional canine in the anterior alveolus.

Because SAM 4341 possesses 6 incisors and lacks precanines it is referred to Glanosuchus macrops.

Scymnosaurus ferox Broom, 1903

Referred specimen

SAM 9084

Material

Badly weathered and laterally compressed skull and lower jaw of a large lycosuchid lacking the right postdentary bones, most of the parietals and squamosals as well as the right side of the snout; with proximal and distal portions of a left humerus; two vertebrae; an atlas fragment; right coracoid and proximal portions of left radius and ulna.

Locality

Rietfontein, Beaufort West.

Collected

L. D. Boonstra.

References

Boonstra 1953c: 54-56,58, Fig. 1

Boonstra 1954a: 71-72, Fig. 2a

Kitching 1977: 42

Comments

Boonstra (1953c) identified this specimen as Scymnosaurus ferox by comparison with the holotype SAM 632 and described and figured the left articular region. He estimated the overall skull length as 375mm, but by taking the effect of distortion into account a skull length of 350mm would be more

realistic.

Five large incisors, all of which are approximately the same size, are present in each premaxilla, with a diastema between the last incisor and the canine. A single large functional canine is present in the anterior canine alveolus of each maxilla. The right maxilla is fractured dorsally, exposing the root of a smaller canine in the posterior alveolus. Three postcanines are present in each maxilla. Diastemas are present behind the first and second postcanines in the left maxilla and probably contained additional teeth. In the right maxilla a diastema can be seen behind the first postcanine but it is also possible that another tooth may have been present behind the last postcanine. The last postcanine on the left is most recently erupted and is much smaller than the other teeth. Serrations are present on all teeth.

Boonstra (1953c) described the angular region of SAM 9084 incorrectly. Additional preparation and staining of the bone has revealed that the unique dorsal notch of the angular described by him is in fact a fracture and that the real notch is located in the usual position between the body of the angular and the reflected lamina. The outer surface of the reflected lamina is badly damaged and contrary to Boonstra (1953c) its posterior margin does not extend to the surangular, nor does it underlap the articular. The suspensorium is weathered and in lateral view it is visible in section. The relative positions of the constituent bones in this region is usual.

Further preparation and staining has shown that the dorsal spur on the posterior aspect of the articular as described by Boonstra (1953c) is not present and neither is the depression on the medial surface of the quadrate condyle for the contact with the distal end of the stapes.

Because of the presence of 5 upper incisors and the low number of upper postcanines the specimen can be identified as a lycosuchid but because of the lack of additional diagnostic features SAM 9084 can only be placed as Lycosuchidae *incertae sedis*.

Scymnosaurus major Boonstra, 1954

Holotype

SAM 9005

Material

Weathered and laterally crushed preorbital portion of a very large lycosuchid with anterodorsal portions of both lower jaw rami; partial occiput; left radius and ulna; interclavicle with portions of clavicle and vertebrae; distal ends of both humeri; distal fragment of scapula; two possible sacral ribs of a very large vertebrate; 6 small bone fragments.

Locality

Kleinkoedoeskop, Beaufort West.

Collected

L. D. Boonstra.

Original generic diagnosis

See holotype of Scymnosaurus ferox for generic diagnosis of Scymnosaurus.

Original specific diagnos

There are 2 to 3 postcanines; mentum fairly upright and symphysis fairly strong; maximum skull length 450-474mm (as reconstructed); frontal excluded from orbital border (after Boonstra 1954a: 73).

References

Boonstra 1954a: 73, Fig. 3

Haughton and Brink 1955: 134

Kuhn 1965: 100

Kitching 1977: 38

Comments (Fig. 78a-b)

In the type description of Scymnosaurus major Boonstra (1954a) noted that portions of the pectoral girdle were present with the specimen. Later (Boonstra 1964) in his description of the girdles and limbs of the pristerognathid Therocephalia he listed with the anterior half of the skull an interclavicle, proximal parts of both clavicles, distal ends

of both humeri and a complete radius and ulna. Associated also with the specimen is a weathered pair of exceptionally massive bones which appear not to belong with the specimen. Cluver (pers. comm.) is of the opinion that these elements may possibly be sacral ribs of a large tetrapod. A partial occiput of a large scylacosaurid, not mentioned by Boonstra (1954a), is also included under this number. Because there is no contact between the occipital fragment and the preorbital portion of the skull it cannot be reasonably assumed that they represent a single skull.

The holotype of Scymnosaurus major is fragmentary but with a preorbital length of 210mm it possibly represents the largest therocephalian known. In ventral view a section through the symphysis shows that it is unankylosed and that the anterior portion of the splenial is not thickened as in gorgonopsians. The roots of three lower incisors are visible in the right dentary. The above features, together with the immense size of the specimen precludes it from being an advanced therocephalian or a gorgonopsian.

Five large upper incisors are present. In both maxillae the huge canines appear to be located in the anterior alveolus since they lie directly behind the last incisor and each is followed by a large diastema. In each maxilla two postcanines are present.

According to Boonstra (1954a) the mentum is fairly upright and the symphysis fairly strong. The anteroventral portion of the mentum is however missing and what can be seen

of the symphysis appears usual for early therocephalians.

Additional preparation and staining of the interorbital portion of the skull roof has revealed that contrary to Boonstra (1954a) the frontal is not excluded from the dorsal border of the orbit. It appears that in older specimens, such as the type of Scymnosaurus major the dorsal border of the orbit becomes thickened and rugose, often obscuring the sutures between bones. Detailed preparation is therefore needed to determine contacts between bones, as for example with the interorbital portion of the skull roof of Lycosuchus keyseri GS C60 (Figs 61m,61n).

A shallow preorbital depression is present. On the right it has been distorted and appears unnaturally deep. The outer surfaces of the maxillae and nasals are rugosely pitted and a number of small foramina and sulci are seen.

According to Boonstra (1954a) the orbits lie partly in the anterior half of the skull. Since the postorbital portion of the skull is missing, the overall length of the skull can only be estimated and the exact position of the orbit is open to speculation.

Because of the lack of distinguishing features as well as the fact that sheer size is not diagnostic in this case Scymnosaurus major is regarded as a nomen dubium and placed as Lycosuchidae incertae sedis.

Scymnosaurus major Boonstra 1954

Referred specimen

SAM 10556

Material

Extremely badly weathered preorbital portion of a large lycosuchid skull with the anterior portions of both lower jaw rami.

Locality

Knoffelfontein, Beaufort West.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 73, Fig. 2b

Kitching 1977: 38

Comments

An extremely poor specimen with 5 incisors and at least 3 postcanines. In the left maxilla the root of a replacement canine is visible.

The specimen has been crushed laterally and shows no specific diagnostic features. The right septomaxilla is however well preserved and a large maxillo-septomaxillary foramen is present. The posteroventral border of the

septomaxilla is depressed inward to form the anterior portion of the maxillo-septomaxillary foramen. Within this depression the posterior septomaxillary foramen is visible.

Because of the lack of diagnostic features this specimen can only be placed as Lycosuchidae *incertae sedis*.

Scymnosaurus watsoni Broom, 1915

Holotype

BMNH R4100

Material

Badly weathered and distorted skull of a scylacosaurid therocephalian lacking left postorbital half or skull, the entire premaxillary region and most of the right squamosal.

Locality

Uitkyk, Prince Albert.

Collected

T. Bain.

Original generic diagnosis

"The principal characteristics of the skull are the great size of the temporal fossae, the narrowness of the snout and the presence of a narrow high parietal crest" (Broom 1915b:

169).

Original specific diagnosis

As for genus.

References

Watson 1914b: 1035-1038, Fig. 7

Broom 1915b: 169-171, Fig. 6

Watson 1921: 80-84, Fig. 23,24

Haughton 1924: 78,101

Broom 1932: 59-60, Fig. 18A,B

Boonstra 1934: 223-226, Fig. 6-8

Kuhn 1937a: 122-123

Boonstra 1954a: 84

Haughton and Brink 1955: 134

Lehman 1961: Fig. 1

Kuhn 1965: 100

Müller 1968: Fig. 623a,b,c

Boonstra 1969b: 56

Kitching 1977: 45

Comments (Fig. 79)

This specimen is in an extremely poor condition in that it is badly weathered and much distorted. In dorsal view the temporal fenestra appears abnormally wide and in lateral view the temporal arch is unnaturally elevated. In addition the height of the sagittal crest appears enhanced.

Because the anterior portion of the snout is missing the number of incisors is unknown. The palate is unfortunately too poor to determine the presence of teeth on what appears to have been the pterygoid bosses. Both Watson (1914b) and Boonstra (1934), however, illustrated the specimen with pterygoid bosses containing teeth. Conversely the transverse processes of the pterygoids are devoid of teeth. Both the interpterygoid vacuity and the basal tubera are small. Boonstra (1934) figured the specimen with 3 upper postcanines, the last postcanine in line with the posterior margin of the internal choana.

Additional preparation has also revealed the presence of a contact between the squamosal and the prootic immediately anterior to the posttemporal fenestra, thus forming a pterygo-paroccipital foramen as in scylacosaurids and advanced therocephalians.

BMNH R4100 was initially described by Watson (1914b) who doubtfully placed it as Lycosuchus. Broom (1915b) referred it to Scymnosaurus watsoni, in which taxon it was retained, albeit doubtfully, by Broom (1932). Initially Boonstra (1934) recognised the taxon but later (Boonstra 1954a p. 84) referred it to Pristerosaurus, only to reinstate the specimen as Scymnosaurus watsoni at a later date (Boonstra 1969b).

The paucity of diagnostic features at generic level precludes a precise taxonomic placement of this specimen. On the available features BMNH R4100 can only be diagnosed as Scylacosauridae incertae sedis. Scymnosaurus watsoni is

therefore a nomen dubium.

Scymnosaurus sp. incertae sedis Boonstra, 1954

Referred specimen

SAM 8999

Material

Badly weathered anterior extremity of a lycosuchid snout.

Locality

Unknown.

Collected

Unknown.

References

Boonstra 1954a: 74.

Comments

This specimen is very poor but the loose symphysis shows that it is a therocephalian and the tooth serrations indicate that it is a member of the early Therocephalia. Because it has only 5 upper incisors it may be placed as Lycosuchidae incertae sedis.

Scymnosaurus sp. *incertae sedis* Boonstra, 1954

Referred specimen

SAM 9126

Material

Badly weathered anterior portion of a theriodont snout.

Locality

Voëlfontein, Prince Albert.

Collected

L. D. Boonstra.

References

Boonstra 1954a: 74

Kitching 1977: 46

Comments

This specimen is too poor to classify. The presence of 5 upper incisors, some of which are serrated, indicates that it is either a gorgonopsian or an early therocephalian. It is therefore regarded here as Theriodontia *incertae sedis*.

Scymnosaurus sp. *incertae sedis* Boonstra, 1954

Referred specimen

SAM 11459

Material

Badly weathered anterior extremity of an early therocephalian snout and lower jaw with portions of a carpus and tarsus.

Locality

Buffelsvlei, Beaufort West.

Collected

L. D. Boonstra & J. Marais.

References

Boonstra 1954a: 74

Kitching 1977: 34

Comments

This specimen is extremely poor but the sloping mentum and loose symphysis indicate that it is a therocephalian. Serrations, present on one lower postcanine, show that it is an early therocephalian. Contrary to Boonstra (1954a) the number of incisors are indeterminate and the specimen can only be placed as early Therocephalia *incertae sedis*.

Scymnosaurus sp. *incertae sedis* Boonstra, 1954

Referred specimen

SAM 11833

Material

Badly weathered early therocephalian snout fragment with anterior portions of both lower jaw rami.

Locality

Lammerkraal, Prince Albert.

Collected

Presented by Mr Pienaar, according to the catalogue. Boonstra (1954a) stated that the specimen was collected by himself and Pienaar.

References

Boonstra 1954a: 74

Kitching 1977: 40

Comments

The symphysis shows that the specimen is a therocephalian and serrations on one lower incisor indicate that it is an early therocephalian. Because the number of incisors are indeterminate and no other diagnostic features are apparent the specimen is regarded as early Therocephalia *incertae*

sedis.

Scymnosaurus sp. incertae sedis Boonstra, 1954

Referred specimen

SAM 11961

Material

Badly weathered anteroventral portion of an early therocephalian snout and lower jaw.

Locality

Dikbome, Laingsburg.

Collected

L. D. Boonstra

References

Boonstra 1954a: 74

Kitching 1977: 35

Comments

The sloping mentum and loose symphysis of the specimen indicate that it is a therocephalian. Serrations on the teeth show that it is an early therocephalian. Five upper incisors appear to have been present and in view of the absence of

additional diagnostic features the specimen can only be placed as Lycosuchidae *incertae sedis*.

Tamboeria maraisi Seeley, 1904

Holotype

BMNH R3348

Comments

The holotype consists of an isolated, weathered, cervical vertebra collected by H.G. Seeley at Tamboerfontein, Beaufort West. An additional dorsal vertebra (R3349) is referred to *Tamboeria* but not included in the holotype. Because of the lack of diagnostic features the specimen has on the whole been ignored in the literature, but Watson & Romer (1956) placed it as Therapsida *incertae sedis*. Romer (1956,1966), Vjuschkov (1964) and Kuhn (1965) included it in the Pristerognathidae, the former two authors albeit doubtfully. Since it would be difficult even to establish its possible subordinal status, *Tamboeria maraisi* is here regarded as a *nomen dubium*.

Theriodesmus phylarchus Seeley, 1888

Holotype

BMNH 49392

Material

Natural mould of a theriodont forelimb with portions of the tibia and fibula and an impression of a caudal vertebra.

Locality

Klipfontein, Fraserburg.

Collected

T. Bain.

Comments (Fig. 80)

This specimen was described by Seeley (1888) as a primitive, generalised mammal. Broom (1907c, 1907d) regarded it as a therocephalian but later (1914) stated that *Theriodesmus* is 'nearly certainly a gorgonopsian and possibly the same as *Aelurosaurus*. Because of the lack of diagnostic features it has, over the years, been largely ignored in most general taxonomic reviews of the Therocephalia viz. Haughton (1924), Broom (1932) and Haughton and Brink (1955), but has been doubtfully regarded as Therocephalia *incertae sedis* by

Watson and Romer (1956) and Kuhn (1965), and as a member of the Pristerognathidae by Von Huene (1956).

The locality of Klipfontein, Fraserburg lies above the Nuweveld escarpment and therefore falls within the *Cistecephalus* Zone (*sensu* Kitching 1977). Because of this the chance of the limb belonging to an early therocephalian is remote. On balance, the fragmentary nature of the specimen, the general similarity of limb elements among the advanced Therocephalia and the fact that the proximal portion of the ulna seems to resemble that of a gorgonopsian rather than an advanced therocephalian, a view supported by Boonstra (1964), precludes a more precise taxonomic placement than Gorgonopsia *incerae sedis*. *Theriodesmus phylarchus* is therefore a *nomen dubium*.

Therioides cyniscus Boonstra, 1953

Holotype

SAM 11888

Material

Badly weathered and laterally crushed skull of a scylacosaurid therocephalian lacking postorbital and temporal arches, and most of the skull roof and occiput; with portion of pectoral girdle, right humerus, right radius, right ulna and part of right manus; proximal portion of left humerus and

several vertebrae.

Locality

Vindraersfontein, Beaufort West.

Collected

L. D. Boonstra.

Original generic diagnosis

Pristerognathid with dental formula of I.6,C.1,Pc.6-7; post-canines slender and small; mentum fairly strong and squarish; quadrate situated far ventrally; maximum length about 270mm; snout as high as broad (55mm); orbit well in posterior half of skull (after Boonstra 1953c: 58).

First emended generic diagnosis

Fairly large pristerognathids with dental formula of I.6,C.1,Pc.6; incisors subequal, moderately long and slender; canine long and strong; postcanines well spaced, small and slender; skull fairly large (maximum length 275mm, as reconstructed); preorbital depression fairly deep but without abrupt margins and shallowing in the direction of the canine; frontal probably just entering the orbital border; snout as broad as high, only slightly narrowed behind canines; orbits well in posterior half of skull; mandibular symphysis fairly weak, but mentum fairly upright; quadrate situated very low down in skull, far ventral of occipital condyle (after

Boonstra 1954a: 84-85).

Second emended generic diagnosis

Dental formula I.6,C.1,Pc.6; postcanines small, slender and well spaced; descending process of squamosal very deep so that lower jaw articulation is situated for ventrally (after Boonstra 1969b: 52).

Original specific diagnosis

As for genus.

First emended specific diagnosis

As for genus.

Second emended specific diagnosis

As for genus.

References

Boonstra 1953c: 58,60, Fig.II

Boonstra 1954a: 85-86, Fig. 8

Haughton & Brink 1955: 134

Romer 1956: 698

Von Huene 1956: 317

Watson and Romer 1956: 69

Lehman 1961: 227, Fig. 3D

Boonstra 1963: 178

Vjuschkov 1964: 276

Kuhn 1965: 100-101

Boonstra 1969b: 52,61

Kemp 1972a: 11

Kitching 1977: 45

Comments (Fig. 81a-c)

This specimen is badly preserved but most of the teeth can be seen clearly. Contrary to Boonstra (1953c, 1954a) there are 7 upper incisors in the left premaxilla. In the right premaxilla only 6 incisors can be seen. Additional prepration has revealed the existence of a minute marginal precanine in each maxilla (Fig. 81c). The large, serrated, functional canine appears to be located in the anterior alveolus on both sides of the snout. Contrary to the emended diagnosis of Boonstra (1954a) there are 7 postcanines in each maxilla instead of 6. These teeth do not appear slender and small as stated in the first and second emended generic diagnoses. In addition, the mean tooth size may vary within certain limits because the dentition is replaced periodically. Compared with other specimens it can also be seen that the mentum of Theriodes cyniscus is not unusually strong or squarish.

The specimen is fractured through the orbits and the fit is not exact. As the result of distortion the ventral border of the lower jaw has an arched appearance and this has artificially depressed the jaw articulation and the position of the quadrate.

Because of the lateral compression the snout has been narrowed and in this state the height and width is about equal (55mm). Boonstra (1953c, 1954a) regarded this condition as diagnostic but it follows that if the snout was restored to its original dimensions it would be broader than high which is the usual condition in the early Therocephalia.

The anterior borders of the orbits lie almost exactly on the transverse midline as in all scylacosaurids.

According to Boonstra (1953c) the posterior edge of the dentary sweeps sharply in a posterior direction and is directed more towards the squamosal than towards the temporal opening. Because of the poor fit between the middle and posterior portions of the skull as well as the distortion present in the specimen, this feature is open to interpretation and cannot be verified.

The angular is badly weathered but remnants of the usual pentaradiate ridge system, with the accompanying depressions, is apparent. Boonstra (1953c, Fig. 11a) is incorrect in stating that the ventral border of the angular proper projects below the reflected lamina. Additional preparation has shown that the section of bone in question is actually part of the reflected lamina. Boonstra (1953c) is correct in that the bone surface within the notch of the reflected lamina is part of the angular proper. His generalised description of the relationships of the postdentary bones, jaw articulation and the squamosal is correct. The posteroventral margin of the squamosal is notched in a similar fashion as that of the type

of Lycedops scholtzi.

Boonstra (1953c) regarded the tympanic membrane to have been attached to the slightly concave ventral border of the posterior descending flange of the squamosal and the ventrodistal corner of the paroccipital process. Later (p. 63), when describing the type of Pristerognathoides paucioridens, he also considered the internal border of the quadratic condyle as an additional area of attachment for the tympanum.

Boonstra (1953c) described and figured the stapes. All that is presently attached to the specimen is a small fragment of bone in the region of the foramen ovalis which may be a stapedial remnant. It is presumed that the stapes was in place at the time of description but has been subsequently lost.

Boonstra's (1954a, 1969b) emended diagnoses, like the original diagnosis, are based on non-diagnostic features since the actual number of incisors differ from that of the diagnosis, the incisors always are subequal and the canine is always long and strong but may vary in size, depending on its stage of development in the replacement cycle.

The shallow preorbital depression on the right has been enhanced by grinding and is not unique at generic level. Nothing can be said about the entry of the frontal into the orbital border since the interorbital region is almost completely missing.

Therioides cyniscus is therefore based on non-diagnostic

features and since additional preparation has revealed the presence of 7 incisors and a small precanine it is here referred to Scylacosaurus sclateri.

Tigrisuchus simus Owen, 1876

Holotype

BMNH R1721

Comments

Gorgonopsian snout included by Broom (1932) amongst the early Therocephalia.

Trochorhinus vanhoepeni Broom, 1936

Holotype

TM 275

Material

Extremely badly weathered snout and lower jaw fragment of a therocephalian.

Locality

Abrahamskraal, Prince Albert.

Collected

E. C. N. van Hoepen.

Original generic diagnosis

This specimen is clearly a distinct species because in the type of Trochosaurus major the 5 incisors measure 45mm and in Trochosaurus intermedius, described by Haughton, the 5 incisors measure 48mm. In Trochorhinus vanhoepeni the 5 incisors measure 35mm. As the skull is clearly not that of a young animal there can be little doubt that the species is distinct. Then as in T. major there are 4 upper and 5 lower molars, while in this new form there are only 3 upper molars and 4 lower molars, it seems necessary to place it in a new genus (after Broom 1936a: 354).

Original specific diagnosis

As for genus.

References

Broom 1936a: 354

Kuhn 1937a: 122

Romer 1945: 602

Haughton and Brink 1955: 135

Romer 1956: 698

Von Huene 1956: 317

Watson and Romer 1956: 69,89

Lehman 1961: 233

Vjuschkov 1964: 277

Kuhn 1965: 102-103

Romer 1966: 373

Boonstra 1969b: 53,57,61

Kitching 1977: 32

Van den Heever 1980: 116

Comments (Fig. 82a-b)

Because of the fragmentary nature of the specimen it is an extremely bad type. The symphysis is loose and the ventral border of the lower jaw forms a straight line with it. In the left dentary, 3 incisors are present. The remains of 5 upper incisor roots are visible and in each of the damaged maxillae both canine alveoli are seen. In the right maxilla the functional canine appears to have been situated in the posterior alveolus since only the root of the anterior fang is visible. In the left maxilla both canines appear to be about the same size with the anterior tooth probably the functional one.

There appears to be 4 upper postcanines in the right maxilla but the second tooth may be a replacement for the third. The remains of 4 postcanines can be seen in the right dentary.

Nothing else can be determined from this specimen. The measurements given by Broom (1936a) in his generic diagnosis are meaningless in the light of the condition of the specimen. It is also possible that there may have been a greater number

of upper and lower postcanines. The specimen is, however, extremely difficult to prepare and in view of its fragmentary nature would most likely not provide any new information.

Romer (1945) regarded Trochorhinus as a pristerognathid but Haughton and Brink (1955) placed it in the family Lycosuchidae because they considered it to possess two functional canines in each maxilla. Romer (1956) placed Trochorhinus in the Trochosuchidae together with Lycosuchus, Hyaenasuchus and Trochosuchus. Von Huene (1956) regarded Trochorhinus as a pristerognathid, whilst Watson and Romer (1956) followed Romer (1956) as did Lehman (1961). Vjuschkov (1964) and Kuhn (1965) included Trochorhinus with the same specimens as Romer (1956), Watson and Romer (1956) and Lehman (1961), but called the family the Lycosuchidae. Romer (1966) however, grouped the same specimens in a new family, the Trochosauridae (Lycosuchidae) whilst Boonstra (1969b) and Kithing (1977) retained Trochorhinus within the Lycosuchidae. Boonstra (1969b) and Kitching (1977) were correct as the name Lycosuchidae had precedence (Van den Heever, 1980, p. 117). Subsequently Van den Heever (1980) invalidated the then Lycosuchidae and pointed out that the parameters defining the family fell within that of the Pristerognathidae.

All that can therefore be determined about this specimen is that it is an early therocephalian with 5 upper incisors and thus probably referable to the Lycosuchidae. Trochorhinus vanhoepeni is consequently regarded as a nomen dubium.

Trochosaurus dirus Broom, 1936

Holotype

Unknown

Material

Anterior portion of a large early therocephalian skull in sections.

Locality

Unknown.

Collected

Unknown.

References

Broom 1936c: 4-7, Plate 1 Fig. 1-9

Kuhn 1937a: 119

Haughton and Brink 1955: 136

Comments (Fig. 83a-b)

From Fig. 83a it is possible to determine that the specimen was an early therocephalian (3 lower incisors) and probably belonged to the Lycosuchidae (5 upper incisors). However, because of the fragmentary nature of the specimen and the fact that the secitons of the specimen have been lost

Trochosaurus dirus is here regarded as a *nomen dubium*.

Trochosaurus major Broom, 1932

Trochosaurus Haughton, 1915

type species *Trochosaurus intermedius* Haughton, 1915 by monotypy

Trochosaurus major (Broom, 1915)

Trochosuchus major Broom, 1915a: 121, Fig. 9 AMNH 5543

Trochosaurus intermedius Haughton 1915: 55 SAM 2756

Trochosaurus major, Broom 1932: 50 new combination

In the interests of clarity the two type specimens referred to *Trochosaurus major* will be discussed separately.

Trochosaurus intermedius Haughton, 1915

Holotype

SAM 2756

Material

Extremely badly weathered anterior two thirds of a distorted scylacosaurid skull.

Locality

Abrahamskraal, Prince Albert.

Original generic diagnosis

Trochosaurus intermedius lies nearest to Lycosuchus, being distinguished from it by the shallow incisor region of the upper jaw, by the much deeper dentary - characters in which it agrees with Trochosuchus - and by the greater width of the intertemporal region. From Trochosuchus it is distinguished by the fact that the two canines are approximately equal in size, whereas in the older genus, the first canine is of the size of the incisors, and the second canine is considerably larger (after Haughton 1915: 56).

Original specific diagnosis

As for genus.

References

Haughton 1915: 55-56

Haughton 1924: 78,101

Broom 1932: 50,51

Kuhn 1937a: 119

Haughton and Brink 1955: 136

Kitching 1977: 32

Comments (Fig. 84a-b)

This specimen is in an extremely bad state of

preservation. In the right premaxilla the roots of 5 incisors are still present and appears to have been the full complement. The snout is weathered to such an extent that the two canine roots in each maxilla are exposed. One postcanine root is visible in the left maxilla and in the right maxilla there are indications of, possibly, 2 postcanines. It appears evident that only a few postcanines were originally present. The nasal process of the septomaxilla is visible, as is a portion of the left postorbital. Although most of the cranial bones can be identified by their location, the specimen is too fragmentary to permit adequate descriptions of these elements.

According to Haughton (1915) the pineal foramen is large. The parietals are so damaged, however, that the dorsal opening of the pineal foramen is missing and its size can consequently not be determined. Haughton also pointed out that the postorbital forms more than half of the upper border of the temporal fenestra. This is incorrect as the remaining portion of the postorbital only meets the parietal in the anterodorsal corner of the temporal fenestra. Contrary to Haughton (1915) the incisors are serrated.

A transverse section across the snout shows no evidence of a crista choanalis. The preorbital length of the skull is approximately 121mm which indicates an original skull length of approximately 242mm. No teeth are visible on any part of the palate which, considering the poor condition of the specimen, is hardly surprising.

Broom (1932) referred both Trochosaurus intermedius

(Haughton, 1915) and Trochosuchus major (Broom, 1915) to Trochosaurus major. He retained Trochosuchus acutus (Broom, 1908a) as a separate taxon because he regarded the anterior canine to be smaller than the posterior one. Broom (1932) did indicate, however, that the specimen may be a juvenile.

Trochosaurus major SAM 2756 is so poor that the diagnosis of Haughton (1915) cannot be verified. Because of the apparent lack of a crista choanalis, the presence of only 5 upper incisors and the generally robust aspect of the skull, it is not a scylacosaurid.

As no additional diagnostic features are present Trochosaurus intermedius is a nomen dubium and is here regarded as Lycosuchidae incertae sedis.

Trochosaurus major Broom, 1915

Holotype

AMNH 5543

Material

Weathered and laterally compressed anterior two thirds of an early therocephalian skull.

Locality

Rietfontein, Prince Albert.

Collected

Unknown.

Original generic diagnosis

See holotype of Trochosuchus acutus for generic diagnosis of Trochosuchus.

Emended generic diagnosis

'While it is at present impossible to say with certainty if the two genera Trochosuchus and Trochosaurus are distinct it will probably be safer provisionally to keep Trochosaurus in a different genus' (after Broom 1932: 51).

Original specific diagnosis

It appears that Broom (1915a) regarded Trochosuchus major specifically distinct from Trochosuchus acutus because the former is the larger.

Emended specific diagnosis

As for genus.

References

Broom 1915a: 121-122, Fig.9

Haughton 1924: 79,101

Broom 1932: 50,51

Boonstra 1934: 227

Boonstra 1935a: 9-10

Kuhn 1937a: 118

Haughton & Brink 1955: 136

Kitching 1977: 42

Comments (Fig. 85a-b)

This specimen is in an extremely poor condition because, not only is the entire outer surface of the skull weathered away, but in large areas the bone has been completely destroyed. In addition both the upper and lower postcanine regions have been extensively damaged by grinding techniques.

Broom (1915a) established this specimen as Trochosuchus major because it was larger than Trochosuchus acutus Broom, 1908. He regarded the maxilla to possess two, large, simultaneously functional canines and discredited the idea that one of these teeth might be a replacement canine. On the whole this specimen is so incomplete that the description of Broom (1915a) is taxonomically meaningless, particularly with reference to the number of upper postcanines which is first stated to be 3 in number and later described as not preserved.

The specimen has the loose symphysis and sloping mentum of a therocephalian. Contrary to Boonstra (1935a) the number of lower incisors is indeterminate. There are no precanine teeth or preparietal bone. A postfrontal is present, the intertemporal region is narrow and the teeth are serrated. There are 5 upper incisors. In the right maxilla the roots of 2 postcanines are present with what appears to be the remnant of an earlier tooth anterior to the first postcanine. Because

of a fracture in the postcanine region and the fact that the alveolar margins of both maxillae have been ground away the actual number of postcanines is indeterminate.

In the left ramus of the lower jaw 4 postcanines are present but it is not possible to determine if they represent the original complement of teeth.

Originally described by Broom (1915a) as Trochosuchus major this specimen was synonymised with Trochosaurus intermedius (Haughton, 1915) by him (Broom 1932) as Trochosaurus major.

The specimen is an early therocephalian as it possesses serrated teeth and a postfrontal bone. The 5 upper incisors indicate that it is a lycosuchid. However, since it lacks diagnostic features below the level of family, Trochosaurus major AMNH 5543 is a nomen dubium and here regarded as Lycosuchidae incertae sedis.

Trochosaurus major Broom, 1915

Referred specimen

BMNH R5747

Material

Badly weathered, partial early therocephalian skull with portion of lower jaw.

Locality

Unknown.

Collected

Purchased from R. Broom.

References

Broom 1932: 50-52, Figs 15a, 16a.

Boonstra 1934: 227-231, Figs 9-11

Boonstra 1935a: 10

Kuhn 1937a: 119

Boonstra 1953c: 63

Kermack 1956: 113-115,121,125,126,127, Fig.11

Müller 1968: Fig. 625a

Comments

This specimen has been treated in acid subsequent to its original description and is in a rather poor state. The incisors region appears to be missing but both Broom (1932) and Boonstra (1934) concurred that the specimen possessed 5 upper incisors. It was referred to Trochosaurus major by Broom (1932) and formed the subject of the figures of the skull as well as most of the description of the genus.

Broom (1932) pointed out the peculiar, forked aspect of the distal portion of the paroccipital process where it contacts the quadrate and the squamosal medial to the ridge

for the external acoustic meatus. This configuration is seen in all early therocephalians and appears to be a general feature of the Therocephalia.

Acording to Broom (1932) evidence of tooth replacement in the upper jaw is seen only amongst the incisors and canines. Boonstra (1934) noted that there was definite evidence that the postcanines were also replaced. The choanae are relatively short and extend posteriorly only to a point in line with the posterior margin of the posterior canine. A pterygo-palatine ridge is present which posteriorly forms a toothless pterygoid boss. At least 6 teeth are present on the transverse process of the pterygoid.

The basisphenoidal tubera are large and form a deep hollow between them, a point also raised by Boonstra (1934). His description of the occiput is essentially correct although he is incorrect in stating that the quadratojugal participates in the jaw articulation. Later (Boonstra 1953c:63) he corrected this statement.

Boonstra's (1934) description of the braincase is correct and usual for the early Therocephalia. However, according to him the epipterygoid is large and broad and differs from that known in Scymnosaurus, Scylacosaurus and Ictidosuchoides where the bone is supposed to be a relatively narrow plate with straight anterior and posterior edges. With many more specimens now available it is clear that the epipterygoid of the early Therocephalia is a flat bone, pinched in the middle and expanded dorsally and ventrally. The so-called broad

epipterygoid of Trochosaurus major was one of the characteristics of the earlier family Lycosuchidae which van den Heever (1980) invalidated. Mendrez (1972a) specifically pointed out that the 'broad' epipterygoid of Trochosaurus major was no broader than that of the type of Ptomalestes avidus SAM 11942. In addition, further preparation of the type of Lycosuchus vanderrieti US D173 has revealed the usual early therocephalian epipterygoid.

The morphology of the palate agrees very well with the condition found in the Lycosuchidae viz. large basal tubera, 5 upper incisors, short choanae, lack of teeth on the pterygoid boss and the presence of teeth on the transverse process of the pterygoid.

Because of the lack of any further diagnostic features Trochosaurus major BMNH R5747 is a nomen dubium and can only be regarded as Lycosuchidae incertae sedis.

Trochosuchus acutus Broom, 1908

Holotype

SAM 1076

Material

Badly weathered and dorsoventrally crushed preorbital portion of a small scylacosaurid therocephalian skull.

Locality

Rietfontein, Prince Albert.

Collected

The Reverend J.H. Whaits.

Original generic diagnosis

'It differs from Aelurosaurus in having 5 incisors, 2 canines, and only 3 or perhaps 4 molars' (Broom 1908a: 366).

Original specific diagnosis

As for genus.

References

Broom 1908a: 366

Broom 1908b: 370,371,372

Haughton 1924: 78

Broom 1932: 52

Broom 1936c: 14

Kuhn 1937a: 119

Romer 1945: 602

Haughton & Brink 1955: 138

Romer 1956: 698

Watson & Romer 1956: 69

Von Huene 1956: 317

Vjuschkov 1964: 277

Kuhn 1965: 103

Kitching 1977: 42

Van den Heever 1980: 116,117, Fig.4

Comments (Fig. 86a-c)

Trochosuchus is badly weathered but tooth serrations are still visible on the first postcanine in the right maxilla as well as the anterior canine on the left. Together with the sloping mentum and the symphysis which forms a straight line with the ventral margin of the dentary, there is no doubt that this specimen is an early therocephalian.

In the left premaxilla 5 incisors are present and this seems to have been the full complement. In the left maxilla two canine roots are preserved. Although the anterior tooth is smaller it is probably the older of the two fangs. This interpretation is supported by the condition in the right maxilla where the anterior canine has already been shed and its replacement is just in the process of erupting. Four postcanines are present in the left maxilla and 3 in the right maxilla. The roots of several small teeth are visible on the transverse processes of the pterygoids as mentioned by Broom (1908a). However, additional preparation has revealed what may be the roots of 3 small teeth in what appears to be the position of the pterygoid boss. The interpterygoid vacuity is seen in section and is a wide opening which is ventrally confluent with the ventral border of the transverse process of the pterygoid, similar to the condition in Lycosuchus vanderrieti.

Broom (1908a, p.366), when describing Hyaenasuchus whaitsi regarded both canines as being simultaneously functional and later the same year, Broom (1908b), grouped the so-called double canined forms Lycosuchus, Trochosuchus and Hyaenasuchus as a seperate 'line of descent'. (Trochosaurus acutus Broom 1907 at his p. 370 is an error, and should read Trochosuchus acutus Broom 1908.) Williston (1925) grouped Trochosuchus with Lycosuchus and Hyaenasuchus in the Lycosuchidae without giving a diagnosis of the family, whereas Haughton (1924) placed the specimen in the Pristerognathidae.

Broom (1932) retained Trochosuchus acutus as a separate taxon but pointed out that it might be an immature specimen. A second specimen regarded by Broom (1936c) as probably Trochosuchus acutus, because it was collected in the same locality and horizon as the type, cannot be diagnosed as such because the specimen consisted, by his own admission only of the considerably weathered posterior third of a moderately large therocephalian skull. Since the specimen possessed a narrow intertemporal region and a postfrontal bone it would appear to have been an early therocephalian.

Romer (1945) grouped Trochosuchus acutus with the Pristerognathidae whereas Haughton & Brink (1955) placed the specimen in a new family, the Akidnognathidae (defined by the possession of one small canine anterior to the large functional canine). Romer (1956) and Watson & Romer (1956) on the other hand, referred the specimen to yet another new family, the Trochosuchidae which also included all the genera

placed by Haughton & Brink (1955) in the Lycosuchidae. Von Huene (1956) retained Trochosuchus with the Pristerognathidae whereas Vjuschkov (1964) and Kuhn (1965) placed Trochosuchus in the Lycosuchidae. Boonstra (1969b) did not mention the specimen whereas Kitching (1977) referred it to the Alopecodontidae. Haughton & Brink (1955) defined the Alopecodontidae as possessing 2 small canines anterior to the large functional canine in the maxilla.

The straight ventral border of the lower jaw and the loose symphysis show that the specimen is a therocephalian. The tooth serrations indicate that it is an early therocephalian and the presence of 5 upper incisors and teeth on the transverse process of the pterygoid argues a close affinity with the Lycosuchidae. The possible presence of teeth on the pterygoid boss as well as is not clear in this instance (see discussion of pterygoid bone in Chapter 4).

Because the specimen is in such a bad state of preservation no additional diagnostic features are evident. Trochosuchus acutus is herefore a nomen dubium and is considered as Lycosuchidae incertae sedis.

Zinnosaurus paucidens Boonstra, 1964

Holotype

SAM 12185

Material

Nearly complete weathered skull distorted by shear; most of left ramus and anterior half of right ramus of lower jaw; complete right humerus; proximal portion of left humerus; right scapulo-coracoid; proximal end of right femur; distal end of right femur; ?tibia; 8 bone fragments.

Locality

Meyerspoort, Beaufort West.

Collected

L.D. Boonstra and H. Zinn.

Original generic diagnosis

Medium-sized pristerognathid with dental formula I.5, C.1, Pc.2; incisors fairly weak and well spaced; postcanines weak and lie far apart; postcanines situated on thin lappet of maxilla clearly demarcated from general maxillary surface; scapula with well developed flange-process on its posterior border immediately above the glenoid for the scapular head of the triceps; glenoid widely open and facing much laterally; humerus with greatly expanded epicondyles, thin and sheetlike; femur with broadly oval caput and strong thickened trochanter (after Boonstra 1964: 122).

Emended generic diagnosis

Medium sized Scymnosaurine with 5 widely spaced, weak

incisors and 2 rather feeble postcanines (after Boonstra 1969b: 50).

Original specific diagnosis

As for genus.

Emended specific diagnosis

As for genus.

References

Boonstra 1964: 122,128,130,143,148-149,161-162,165, Figs 19,28,46d-e

Boonstra 1968: 200

Boonstra 1969b: 50,56,61

Tatarinov 1974: 118

Kitching 1977: 41

Comments (Fig. 87a-b)

In his original diagnosis Boonstra (1964) noted that the bony tubercle present on the posterolateral surface of the scapula above the glenoid was similar to that of the anteosaurid dinocephalian Eccasaurus. Earlier (Boonstra 1955) he had illustrated the same feature in Anteosaurus SAM 5614. The type material of Eccasaurus does not include a scapulo-coracoid but Boonstra (1955) referred SAM 11597 to this taxon. The scapulo-coracoid of this specimen now appears to be missing from the collection. However, because postcranial

material of lycosuchids and scylacosaurids is relatively scarce, supposedly unique features present in single specimens only, cannot be compared with other taxa and their occurence may in fact be much more widespread than is indicated by the available material. In addition, the scope of this investigation is limited to the comparative morphology of the skull and features of the postcranial skeleton are therefore not included.

Contrary to Boonstra (1964) the incisors are neither well spaced nor weak. In the right premaxilla the roots of 5 closely packed teeth, with a large diastema between the last incisor and the canine, is visible. On the right there are also 5 incisors. The fourth incisor which is generally the largest appears to be in the process of replacement and is represented by a relatively small tooth.

A fracture through the canine region reveals the root of the functional canine with its replacement lying medial to it. There is no crista choanalis.

Contrary to Boonstra (1964) 3 postcanines are present in the left maxilla and they are situated on a ventral flange of bone as in Lycosuchus vanderrieti. The right maxilla is damaged in the postcanine region, but it appears that at least 4, if not 5 postcanines were present on the ventral maxillary flange.

The lower portion of the jaw symphysis is damaged and the root of a single canine is visible, in section, in each dentary. Anterior to both canines the roots of 2 lower

incisors are present. In lingual view 4 postcanines are present in the left ramus of the lower jaw whilst 4 but possibly 5 teeth are visible in the right ramus. The lower postcanines as a group are positioned somewhat anterior, relative to the upper postcanines as in Lycosuchus keyseri GS C60.

The specimen has been subjected to shear but the preorbital depression appears shallow and the suborbital bar deep. The interorbital region is wide and a sagittal crest is present.

In ventral view the choanae are short, extending posteriorly only to the level of the upper canines. The pterygoid boss is devoid of teeth but the transverse process of the left pterygoid contains the roots of at least 7 teeth. Some teeth are also present in the transverse process of the right pterygoid. The basal tubera are large.

This specimen is undoubtedly a lycosuchid and because of the presence of a distinct ventral maxillary flange Zinnosaurus paucidens is here regarded as a synonym of Lycosuchus vanderrieti.

6. CLASSIFICATION AND RELATIONSHIPS

As the result of this investigation a large number of features have been identified by which the early Therocephalia can be organised into two discrete taxonomic groups. These taxa are regarded as families for which the names Lycosuchidae and Scylacosauridae are available and considered appropriate. Historically Lycosuchus vanderrieti US D173 has been regarded as the type genus of the Lycosuchidae because, subsequent to the original description of the specimen by Broom (1903a), no other material which can add to the diagnosis of the family has been discovered. The Lycosuchidae as formulated here differs from the family with the same name, previously diagnosed by Haughton & Brink (1955) and Boonstra (1969b). Their diagnoses were invalidated by Van den Heever (1980) as the features then regarded taxonomically relevant were shown to be non-diagnostic, and the Lycosuchidae was consequently considered a junior synonym of the Pristerognathidae. Because new features have been discovered as the result of preparing Lycosuchus vanderrieti US D173 further and investigating additional, recently discovered material in detail, it is now possible to redefine the Lycosuchidae with confidence. The Scylacosauridae was established by Broom (1903b) who not only based the family on Scylacosaurus sclateri SAM 634, but also designated the specimen as the type genus of the Therocephalia. Historically the Scylacosauridae is thus the

valid type family name of the Therocephalia and has precedence over the commonly used name Pristerognathidae.

The differences between the two families can be listed as follows:

1. Snout short and broad.	1. Snout long and narrow.
2. Snout not constricted behind canine region.	2. Snout constricted behind canine region.
3. Anterior border of orbit in front half of skull.	3. Anterior border of orbit on transverse midline of skull.
4. Interorbital region wide.	4. Interorbital region narrow.
5. Suborbital bar broad.	5. Suborbital bar slender.
6. Orbit large.	6. Orbit small.
7. Ventral surface of frontal shallowly grooved to accommodate olfactory lobes of brain.	7. Ventral surface of frontal deeply grooved to accommodate olfactory lobes of brain.
8. No precanines.	8. Precanines 0, 1 or 2.
9. 5 incisors.	9. 6-7 incisors.
10. Upper postcanines few in number (up to 5).	10. Upper postcanines numerous (5-9).

11. Teeth always present on transverse process of pterygoid.	11. No teeth on transverse process of pterygoid (with possible specialization in Lycedops scholtzi.
12. No teeth on pterygoid boss (with the possible exception of Trochosuchus acutus SAM 1076).	12. Teeth on pterygoid boss.
13. Vomerine process lacking on premaxilla.	13. Vomerine process present on premaxilla.
14. Vomer anteriorly vaulted.	14. Vomer not anteriorly vaulted.
15. No ventromedial crest on posterior portion of vomer.	15. Ventromedial crest on posterior portion of vomer.
16. Choana short.	16. Choana long.
17. Crista choanalis absent.	17. Crista choanalis well developed.
18. No anteromedial process on lacrimal within nasal cavity.	18. Anteromedial process on lacrimal within nasal cavity.
19. Ventromedian tubercle on pterygoid.	19. Ventromedian crest on pterygoid.
20. Interpterygoid vacuity wide.	20. Interpterygoid vacuity narrow.
21. Ventral rim of transverse	21. Ventral rim of

process of pterygoid sweeps posteriorly at midline vacuity.	transverse process of pterygoid does not sweep posteriorly at midline vacuity.
22. Basal tuber large.	22. Basal tuber small.
23. Pterygo-paroccipital foramen absent.	23. Pterygo-paroccipital foramen present.
24. Lateral margin of sella turcica bluntly rounded.	24. Lateral margin of sella turcica sharply ridged.**

** As explained in Chapter Four this feature cannot presently be confirmed as diagnostic owing to a lack of material where this region of could be prepared. It is included here only for the sake of completeness.

As a result of the findings of this investigation, some comments can also be made with regard to the extensive cladistic analysis of therapsid relationships recently proposed by Hopson & Barghusen (1986). These authors did, however, point out that their interpretation of the subgroups of the Therocephalia might be subject to change. Their diagnosis of the Therocephalia lists the following features:

A. Suborbital vacuities in palate
B. Stapes lacks stapedial foramen (Convergent with dicynodonts and, apparently, anteosaurids).

C. Well-developed anteroventral ("prootic") process of the squamosal lying anterior to the posttemporal foramen. (It forms most of the anterior border of the pterygo-paroccipital foramen in all therocephalians with the possible exception of pristerognathids; see 24.4.).

D. Vomer moderately expanded and widest at anterior end.(Whaitsiid vomer widest behind its anterior end due to development of unique lateral process. (Convergent 8.2 in part).

E. Fossa for lower canine confluent with internal naris. (Convergent 8.4).

F. Dorsal process of stapes reduced or absent.

A and B are standard and valid therocephalian features.

C needs to be modified as the presence of a pterygo-paroccipital foramen, formed by the lateral process of the prootic and the otic process of the squamosal, has now definitely been established in the Scylacosauridae. This structure is absent in the known Lycosuchidae and is consequently an important feature aligning the Scylacosauridae with the Eutherocephalia rather than with the Lycosuchidae.

D is misleading as the vomer is widest posteriorly and not anteriorly. The statement should read that the portion of the vomer which bridges the choana, is widest anteriorly. This is not a trivial distinction as the comparison with the whaitsiid

vomer further complicates the issue.

E is incorrect as the crown of the lower canine does not fit in a palatal fossa, but a fenestra, in the Lycosuchidae, Scylacosauridae and a number of eutherocephalian taxa. Primitively a large palatal fenestra is present which, as noted by Hopson & Barghusen (1986), is confluent with the choana. With the gradual development of the secondary palate in the Eutherocephalia and the reduction in size of the mandibular canine, the large palatal fenstra is secondarily roofed with bone. Only when this process is completed can the resulting structure be regarded as a fossa.

F is of doubtful validity as the possibility exists that a dorsal process might have been primitively present on the stapes as is indicated in both the Lycosuchidae and the Scylacosauridae. The stapes is most often not present in specimens of the early Therocephalia and information about this bone is therefore incomplete.

The features here regarded diagnostic of the Therocephlia can consequently be listed as follows:

I Suborbital vacuities in palate

II Stapes lacks stapedial foramen

III Vomer moderately expanded with portion dividing the choanae widest anteriorly.

IV Palatal fenestra for lower canine confluent with

internal naris.

V Dorsal process of stapes may be reduced or absent.

Hopson & Barghusen (1986) followed Van den Heever (1980) in recognising the Pristerognathidae as the only family representing the early Therocephalia. They list the Pristerognathidae as the only taxon of a larger group, the Pristerosauria, originally established by Boonstra (1953a) to include the Pristerognathidae, Lycosuchidae, Scylacosauridae, Ictidosuchidae, Whaitsidae (sic), Alopecopsidae, Lycideopsidae and Euchambersidae (sic). The Pristerosauria is regarded by them as the sister group of the Eutherocephalia, a taxon which represents the rest of the Therocephalia(Fig. 88). As the Lycosuchidae and the Scylacosauridae represent discrete taxa the cladogram of Hopson & Barghusen does not portray the natural diversity of the early Therocephalia. Two possible interpretations follow from this statement. Either the Scylacosauridae and the Lycosuchidae are more closely related to one another than to the rest of the Therocephalia or, alternatively, one of them is more closely related to the rest of the Therocephalia than to the other. In the latter case the taxon least closely related to the Eutherocephalia would be the more primitive and would form the the sister group of the rest of the Therocephalia.

The only apparent apomorphy which to unites the Lycosuchidae and the Scylacosauridae as the Pristerosauria (Fig.89) is the presence of three lower incisors in each

mandibular ramus. Additional apomorphies, according to Hopson & Barghusen (1986) are, a prominent vomerine process of the premaxilla which broadly overlaps the ventral surface of the vomer, and a vomer which is transversely expanded beyond the primitive therocephalian condition. The former structure, as has been shown, is absent in the Lycosuchidae but present in the Scylacosauridae, as well as some members of the advanced Therocephalia. The relevance of the latter feature is not entirely clear as the condition of the vomer in Therocephalia more primitive than the Lycosuchidae and the Scylacosauridae is unknown. The presence of a postfrontal, serrated teeth and the lack of a posttemporal fossa in both taxa are plesiomorphic features as is shown by outgroup comparison, although Olson (1968) described a posttemporal fossa in the pelycosaur family Caseidae.

There are no apomorphies indicating a closer relationship between the Lycosuchidae and the Eutherocephalia than between the latter and the Scylacosauridae.

Apomorphies which indicate that the Scylacosauridae should rather be grouped with the Eutherocephalia than the Lycosuchidae are, the presence of a pterygo-paroccipital foramen enclosed by processes of the squamosal and the prootic, a well developed crista choanalis and a ventromedian crest on the pterygoid. On the basis of features 8,10-14,17,19-20 and 23 the Lycosuchidae is shown to be more primitive than the Scylacosauridae.This interpretation is illustrated in Fig. 90 and it is suggested that as the name

Pristerosauria now has the unfortunate connotation that it has been derived from the Pristerognathidae, an invalidated family, and employed to unite primitive taxa which do not form a natural group, the Lycosuchidae should be grouped as the Lycosauria and the Scylacosauridae + Eutherocephalia as the Scylacosauria. Use of the term Pristerosauria should therefore be discouraged.

Diagnoses of the valid genera and species of the Lycosuchidae and the Scylacosauridae have been given in Chapter 5 and are summarised in Fig. 91. The classification is predominantly based on the number and nature of the upper marginal teeth. The Lycosuchidae consistently possess 5 upper incisors, whereas the number varies from 6-7 in the Scylacosauridae. The presence of a ventral maxillary flange is regarded as diagnostic for lycosuchids and is used to distinguish between L. keyseri and L. vanderrieti.

Within the Scylacosauridae the number of upper incisors varies from 6 to 7 in each premaxilla. The lower number is regarded as the more primitive condition. The number of precanines vary from 0 in Glanosuchus macrops and Pristerognathus polyodon to 1 in Ictidosaurus angusticeps and Scylacosaurus sclateri and a maximum of 2 in Pardosuchus whaitsi and Alopecodon priscus. In each case the lower number of precanines is regarded as the more primitive condition.

7 CONCLUSIONS

This investigation has clarified the functional anatomy of the skull in the early Therocephalia and produced a new perspective on the taxonomy of the Therocephalia based on cladistic principles. Although the advantages of employing cladistic methods in palaeontology is well-known, it needs to be pointed out that, irrespective of the method employed when dealing with a fossil species, the taxonomist is handicapped to a certain extent by the lack of soft anatomy. That this may introduce a subjective component in the resultant classification is indicated by the fact that species diversity cannot be recognised solely on osteological features in certain extant animals, a case in point being the haplochromine cichlid fishes of Lake Victoria. Therefore, the number of species recognised in a taxon based only on osteological features, as is the case in this analysis, almost certainly do not fully represent the original diversity of the group. Additional lines of research that have come to light during the course of the analysis, but lie outside the scope of this project, have been identified for future investigation. The conclusions derived from this project can be listed as follows

1. Previous classifications which regard the early Therocephalia (Lycosuchidae + Scylacosauridae) as a single taxon, isolated from the rest of the Therocephalia, are shown to be incorrect. Even though these two families resemble each other superficially in cranial morphology they do not form a natural group which has taxonomic standing. The Lycosuchidae is the only family in a larger group here designated as the Lycosauria. The Scylacosauridae is more closely related to the Eutherocephalia, which includes the rest of the Therocephalia, than to the Lycosauria. The Lycosauria thus forms the sister group of the Scylacosauria (Scylacosauridae + Eutherocephalia).

2. The Lycosuchidae contain two species L. keyseri and L. vanderrieti of which the latter is distinguished by the presence of a unique, ventral maxillary flange.

3. The Scylacosauridae consists of two groups of 3 species each. The first group contains Glanosuchus macrops, Ictidosaurus angusticeps and Pardosuchus whaitsi. The second group contains the species Pristerognathus polyodon, Scylacosaurus sclateri and Alopecodon priscus. All three species in the first group possess 6 upper incisors and are considered more primitive than those in the second group which possess 7 upper incisors. The lack of precanines is considered primitive. In the first

group Glanosuchus macrops is therefore considered more primitive than either Ictidosaurus angusticeps or Pardosuchus whaitsi. Similarly, in the second group, Pristerognathus polyodon is considered more primitive than Scylacosaurus sclateri and Alopecodon priscus.

4. The extensive historical analysis of the taxonomy of the Theriodontia, but especially the Therocephalia, has shown that previous authors have often summarily accepted incorrect conclusions of others. The introduction, without diagnosis, of the family name Pristerognathidae by Haughton (1924) was incorrect and without scientific basis. At the time the names Scylacosauridae and Lycosuchidae were the valid family names. The name Pristerognathidae became imbedded in the literature as a result of authors uncritically accepting the work of others underlining once again the importance of studying material at first hand.

5. Distinct differences are apparent in the cranial morphology of the early Therocephalia and the Gorgonopsia. However, in the broken and weathered anterior portions of snouts that are often found these differences are much more indistinct and difficult to evaluate. Particular attention was therefore given to the morphology of the mentum and the number of lower incisors in the known specimens. It is now consequently

easier to correctly identify these finds.

6. The anterior portion of the snout is a complicated region and has been described in detail. Although limited evidence of the presence of turbinals has been found, the morphology of the cartilaginous nasal capsule is not known. As the lower canines pierce the anterior portion of the palate and project into the nasal cavity the crowns of these teeth probably fitted into cartilaginous sheaths. If this was not the case the respiratory passage would have become clogged with food debris. Some mechanism must therefore have existed to isolate the nasal and oral cavities from each other. A functional interpretation of this region, including the maxillo-septomaxillary foramen and the organ of Jacobson, is therefore necessary.

7. The smooth aspect of the symphysial surface of the dentary indicates that the symphysis was relatively loose and that a limited amount of independent movement was possible between the two rami of the lower jaw. The configuration of the the jaw articulation indicates that the posterior portions of the rami would tend to be deflected outwards as the jaw opened. A loose symphysis would facilitate this movement. An investigation of the functional mechanism of the lower jaw is therefore necessary.

8. The presence of the squamosal sulcus (external acoustic meatus), the morphology of the quadrate, the configuration of the posteroventral margin of the squamosal and the probable presence of a dorsal process on the stapes all indicate that a postquadrate tympanum was present in the primitive Therocephalia. The fact that the stapes may have been too heavy to respond to high frequency air-borne sound indicates the need for a detailed investigation of this area of the skull.

9. No evidence was found to support the presence of sexual dimorphism in either the Lycosuchidae or the Scylacosauridae. The decision not to utilize size as a diagnostic feature, adopted at the outset of this investigation, is consequently upheld.

10. No immediately apparent features have come to light whereby it is possible to contribute meaningfully to the question of the phylogenetic relationship between the Therocephalia from the Southern African Karoo deposits and those from the Permian of the USSR. The latter forms are relatively few in number, fragmentary and often not well-preserved. These conditions complicate comparisons based on the literature and a detailed, first hand study of the forms from the USSR, against the background of the present investigation, is considered a priority.

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9. ALPHABETICAL LIST OF SPECIMENS DISCUSSED IN THE TEXT

Valid taxa are listed in bold lettering in the right hand column.

Akidnognathidae	FMNH UR2462	Unidentified akidnognathid
Akidnognathus parvus	SAM 4021	Akidnognathidae
Alopecideops gracilis	SAM 4997	Scylacosauridae incertae sedis
Alopecodon minor		See Alopecondon priscus
	BMNH R5750	
Alpecodon priscus	SAM 920	VALID
	SAM 921	Scylacosauridae incertae sedis
	SAM 1209	Early Therocephalia
		see discussion of A. priscus
	SAM 920	
	AMNH 5569	VALID
	BMNH R5750	Scylacosauridae incertae sedis
Alopecodon rugosus		See Alopecodon priscus SAM 921
Alopecognathus angusticeps	AMNH 5559	Glanosuchus macrops
	SAM 9112	Glanosuchus macrops
Alopecognathus angustioriceps	SAM 9342	Glanosuchus macrops
Alopecognathus megalops	TM 1491	nomen dubium Scylacosauridae incertae sedis
Alopecognathus minor		See holotype of Pristerognathoides minor
Alopecognathus skinneri		See Karroowalteria skinneri

Alopecorhinus parvidens		AMNH 5503 nomen dubium
Anna petri		See Annatherapsidus petri
Annatherapsidus petri		PIN 2005/1993 See introduction
Arctosuchus tigrinus	BMNH R1719	Gorgonopsia (Theriodontia incertae sedis Sigogneau 1970)
Arnognathus parvidens	SAM 1069	nomen dubium Scylacosauridae incertae sedis
Broomisaurus planiceps	AMNH 3752	Gorgonopsia
Cerdodon tenuidens	BMNH 49420	nomen dubium early Therocephalia incertae sedis
Chthonosaurus velocidens	PIN 521/1	See introduction
Cynariognathus gallowayi	TM 266	Glanosuchus macrops
Cynariognathus paucioridens	SAM 1080	Theriocephalia incertae sedis
	SAM 11560a	Scylacosauridae incertas sedis
	SAM 11586	Scylacosauridae incertae sedis See also same number as Pristerognathus sp.
Cynariognathus platyrhinus	AMNH 5502	nomen dubium Scylacosauridae incertae sedis
	BMNH R4097	Scylacosauridae incertae sedis
Cynariognathus seeleyi		UM 1934 VIII 30 nomen dubium Scylacosauridae incertae sedis
Cynariognathus sp.	SAM 3713	Glanosuchus macrops
	SAM 9088a	early Therocephalia incertae sedis
	SAM 11968	Glanosuchus macrops

Eriphostoma microdon	AMNH 5524	Gorgonopsia (Theriodontia incertae sedis Sigogneau 1970)
Glaucosuchus		error for Glanosuchus Von Huene 1956:316
Glanosuchus macrops	SAM 637	VALID
	SAM 903	VALID
	SAM 11843	VALID
	SAM 11964	VALID
	GS C63	Unidentified Scylacosaurid probably Glanosuchus macrops
	GS M796	VALID
	GS RS962	VALID
Hexacynodon purlinensis	PIN 1538/6	See introduction
Hofmeyria atavus	TM 254	Hofmeyriidae
Hyaenasuchus whaitsi	SAM 1079	Lycosuchus vanderrieti
Hyaenosuchus		See Hyaenasuchus
Hyorhynchus platyceps		BMNH R872 Scylacosauridae incertae sedis
Ictidoparia brevirostris		no number; type lost nomen dubium
Ictidosaurus angusticeps	SAM 630	VALID
	AMNH 5527	Gorgonopsia
Karroowalteria skinneri	BPI 220	Glanosuchus macrops
Lycedops scholtzi	MM 4499	Scylacosauridae incertae sedis
Lycosaurus pardalis	BMNH R1717	Gorgonopsia (Theriodontia incertae sedis Sigogneau 1970)
Lycosuchus mackayi	SAM 633	nomen dubium Theriodontia incertae sedis

Lycosuchus vanderrieti	US D173	VALID
	GS M793	VALID
Lycosuchus keyseri	GS C60	NEW SPECIES
Maraisaurus parvus	SAM 11944	see Pristerognathoides parvus
Mirotenthes digitipes	UCMP 40467	Hofmeyriidae
Moschorhinus kitchingi	BMNH R5689	Akidnognathidae
Moschorhinus warreni	NM 188 (TN 741)	Akidnognathidae
Moschowhaitsia vjuschkovi	PIN 1190/20	See introduction
Notaelurodon kitchingi	TM 272	advanced therocephalian
Pardosuchus whaitsi	SAM 1077	VALID
Porosteognathus efremovi	PIN 157/19	see introduction
Pristerognathoides minor	SAM 3415	Glanosuchus macrops
	SAM 3435	Glanosuchus macrops
	SAM 4332	Glanosuchus macrops
	SAM 11891	Scylacosauridae incertae sedis
Pristerognathoides parvus	SAM 3611	nomen dubium Scylacosauridae incertae sedis
	SAM 11944	Scylacosauridae incertae sedis
Pristerognathoides peyeri	UM 1936 II 9	Glanosuchus macrops
Pristerognathoides roggeveldensis	SAM 9356a	Glanosuchus macrops
Pristerognathoides vanderbyli	MM 5139	Glanosuchus macrops
Pristerognathoides vanwyki	SAM 6533	Scylacosauridae incertae sedis
	SAM 11689	Scylacosauridae incertae sedis
	SAM 11893	Glanosuchus macrops
Pristerognathus baini	SAM 583	Glanosuchus macrops
Pristerognathus minor		See Pristerognathoides minor

Pristerognathus peyeri		See Pristerognathoides peyeri
Pristerognathus platyrhinus		See Cynariognathus platyrhinus
Pristerognathus polyodon		BMNH R2581 VALID
Pristerognathus vanderbyli		See Pristerognathoides vanderbyli
Pristerognathus vanwyki		See Pristerognathoides vanwyki
Pristerognathus sp.	SAM 631	Pristerognathus polyodon
	SAM 751	Lycosuchidae incertae sedis
	SAM 752	?Therocephalia incertae sedis
	SAM 1075	Scylacosauridae incertae sedis
	SAM 1213	Dinocephalia incertae sedis
	SAM 3432	?Glanosuchus macrops
	SAM 9015	Gorgonopsia
	SAM 9084a	Pardosuchus whaitsi See also description of two additional snouts, one centrum and one humerus included with the specimen.
	SAM 9111	Pardosuchus whaitsi
	SAM 11456	Glanosuchus macrops
	SAM 11586	Scylacosauridae incertae sedis See also same number as Cynariognathus paucioridens
	SAM 11842	early Therocephalia incertae sedis
	SAM 11848	Pristerognathus polyodon
	SAM 11871	Glanosuchus macrops
	SAM 11872	Scylacosauridae incertae sedis

	SAM 11873	Scylacosauridae *incertae sedis*
	SAM 11874	*Glanosuchus macrops*
	SAM 11875	?Ictidorhinid
	SAM 11876	*Glanosuchus macrops*
	SAM 11936	Lycosuchidae *incertae sedis*
	SAM 11956	?Ictidorhinid
	SAM 11957	*Ictidosaurus angusticeps*
	SAM 11960	Scylacosauridae *incertae sedis*
	SAM 11963	*Glanosuchus macrops*
	SAM 11965	Theriodontia *incertae sedis*
	SAM 11966	lost
	SAM 11967	*Glanosuchus macrops*
Pristerosaurus microdon	SAM 9083	*nomen dubium*, Scylacosauridae *incertae sedis*
Pristerosaurus watsoni		See *Scymnosaurus watsoni*
Ptomalestes avidus	SAM 11942	*Pristerognathus polyodon*
	SAM 9012a	lost
	SAM 11460	*Glanosuchus macrops*
Scylacoides ferox	AMNH 5558	Gorgonopsia
Scylacorhinus falkenbachi	AMNH 5560	See *Scylacosaurus sclateri*
Scylacosaurus sclateri	SAM 634	VALID
	AMNH 5560	VALID
	BMNH R4055	VALID
Scylacosuchus orenburgensis	PIN 2628/1	See introduction
Scymnosaurus ferox	SAM 632	*nomen dubium*, Lycosuchidae *incertae sedis*
	SAM 3430	Lycosuchidae *incertae sedis*

	SAM 4341	Glanosuchus macrops
	SAM 9084	Lycosuchidae incertae sedis
Scymnosaurus major	SAM 9005	nomen dubium Lycosuchidae incertae sedis
	SAM 10556	Lycosuchidae incertae sedis
Scymnosaurus warreni		See Moschorhinus warreni
Scymnosaurus watsoni	BMNH R4100	nomen dubium Scylacosauridae incertae sedis
Scymnosaurus sp.	SAM 8999	Lycosuchidae incertae sedis
	SAM 9126	Theriodontia incertae sedis
	SAM 11459	early Therocephalia incertae sedis
	SAM 11833	early Therocephalia incertae sedis
	SAM 11961	Lycosuchidae incertae sedis
Tamboeria maraisi	BMNH R3348	nomen dubium Therapsida incertae sedis
	BMNH R3349	Therapsida incertae sedis
Theriodesmus phylarchus	BMNH 49392	nomen dubium Gorgonopsia incertae sedis
Therioides cyniscus	SAM 11888	Scylacosaurus sclateri
Tigrisuchus simus	BMNH R1721	Gorgonopsia (Theriodontia incertae sedis Sigogneau 1970)
Trochorhinus vanhoepeni	TM 275	nomen dubium Lycosuchidae incertae sedis
Trochosaurus dirus	no number	type lost nomen dubium

		?Lycosuchidae
Trochosaurus intermedius		See Trochosaurus major
Trochosaurus major	SAM 2756	nomen dubium Lycosuchidae incertae sedis
	AMNH 5543	nomen dubium Lycosuchidae incertae sedis
	BMNH R5747	nomen dubium Lycosuchidae incertae sedis
Trochosuchus acutus	SAM 1076	nomen dubium Lycosuchidae incertae sedis
Trochosuchus major		See Trochosaurus major
Walteria skinneri		See Karroowalteria skinneri
Zinnosaurus paucidens		SAM 12185 Lycosuchus vanderrieti

10. NUMERICAL LIST OF SPECIMENS

AMNH			
	3752	Broomisaurus planiceps	Gorgonopsia
	5502	Cynariognathus platyrhinus	nomen dubium Scylacosauridae incertae sedis
	5503	Alopecorhinus parvidens	nomen dubium
	5524	Eriphostoma microdon	Gorgonopsia (Theriodontia incertae sedis Sigogneau 1970)
	5527	Ictidosaurus angusticeps	Gorgonopsia
	5543	Trochosaurus major	nomen dubium Lycosuchidae incertae sedis
	5558	Scylacoides ferox	Gorgonopsia incertae sedis
	5559	Alopecognathus angusticeps	Glanosuchus macrops
	5560	Scylacorhinus falkenbachi	See Scylacosaurus sclateri
	5569	Alopecodon priscus	VALID
BMNH			
	R872	Hyorhynchus platyceps	Scylacosauridae incertae sedis
	R1717	Lycosaurus pardalis	Gorgonopsia (Theriodontia incertae sedis Sigogneau 1970)
	R1719	Arctosuchus tigrinus	Gorgonopsia (Theriodontia incertae sedis Sigogneau 1970)
	R1721	Tigrisuchus simus	Gorgonopsia (Theriodontia incertae sedis Sigogneau 1970)
	R2581	Pristerognathus polyodon	VALID
	R3348	Tamboeria maraisi	nomen dubium Therapsida incertae sedis
	R3349		Therapsida incertae sedis
	R4055	Scylacosaurus sclateri	VALID
	R4097	Cynariognathus platyrhinus	Scylacosauridae incertae sedis
	R4100	Scymnosaurus watsoni	nomen dubium Scylacosauridae incertae sedis
	R5689	Moschorhinus kitchingi	Akidnognathidae
	R5747	Trochosaurus major	nomen dubium Lycosuchidae incertae sedis
	R5750	Alopecodon priscus	Scylacosauridae incertae sedis See Alopecodon

			priscus SAM 921
	49392	Theriodesmus phylarchus	nomen dubium
			Gorgonopsia incertae sedis
	49420	Cerdodon tenuidens	nomen dubium early Therocephalia incertae sedis
BPI			
	220	Karroowalteria skinneri	Glanosuchus macrops
FMNH			
	UR2462		Unidentified akidnognathid
GS			
	273		Unidentified scylacosaurid
	C60	Lycosuchus keyseri	NEW SPECIES
	C63		Unidentified scylacosaurid, probably Glanosuchus macrops
	M793	Lycosuchus vanderrieti	VALID
	M796	Glanosuchus macrops	VALID
	RS330		Unidentified scylacosaurid
	RS962	Glanosuchus macrops	VALID
MM			
	4499	Lycedops scholtzi	Scylacosauridae incertae sedis
	5139	Pristerognathoides vanderbyli	Glanosuchus macrops
NM			
	188 (TN 741)	Moschorhinus warreni	Akidnognathidae
PIN			
	157/19	Porosteognathus efremovi	See introduction
	521/1	Chthonosaurus velocidens	See introduction
	1190/20	Moschowhaitsia vjuschkovi	See introduction
	1538/6	Hexacynodon purlinensis	See introduction
	2005/1993	Annatherapsidus petri	See introduction
	2628/1	Scylacosuchus orenburgensis	See introduction
SAM			
	583	Pristerognathus baini	Glanosuchus macrops
	630	Ictidosaurus angusticeps	VALID
	631	Pristerognathus sp.	Pristerognathus polyodon
	632	Scymnosaurus ferox	nomen dubium Lycosuchidae incertae sedis
	633	Lycosuchus mackayi	nomen dubium (Theriodontia incertae sedis)
	634	Scylacosaurus sclateri	VALID
	637	Glanosuchus macrops	VALID
	751	Pristerognathus sp.	Lycosuchidae incertae sedis
	752	Pristerognathus sp.	?Therocephalia incertae sedis
	903	Glanosuchus macrops	VALID
	920	Alopecodon priscus	VALID
	921	Alopecodon priscus	Scylacosauridae

		incertae sedis
1069	Arnognathus parvidens	nomen dubium
		Scylacosauridae
		incertae sedis
1075	Pristerognathus sp.	Scylacosauridae
		incertae sedis
1076	Trochosuchus acutus	nomen dubium
		Lycosuchidae
		incertae sedis
1077	Pardosuchus whaitsi	VALID
1079	Hyaenasuchus whaitsi	Lycosuchus
		vanderrieti
1080	Cynariognathus paucioridens	Therocephalia
		incertae sedis
1209	Alopecodon priscus	Early
		therocephalian; see
		discussion of
		A. priscus SAM 920
1213	Pristerognathus sp.	Dinocephalia
		incertae sedis
2756	Trochosaurus major	nomen dubium
		Lycosuchidae
		incertae sedis
3415	Pristerognathoides minor	Glanosuchus macrops
3430	Scymnosaurus ferox	Lycosuchidae
		incertae sedis
3432	Pristerognathus sp.	?Glanosuchus macrops
3435	Pristerognathoides minor	Glanosuchus macrops
3611	Pristerognathoides parvus	nomen dubium
		Scylacosauridae
		incertae sedis
3713	Cynariognathus sp.	Glanosuchus macrops
4021	Akidnognathus parvus	Akidnognathidae
4332	Pristerognathoides minor	Glanosuchus macrops
4341	Scymnosaurus ferox	Glanosuchus macrops
4997	Alopecideops gracilis	Scylacosauridae
		incertae sedis
6533	Pristerognathoides vanwyki	Scylacosauridae
		incertae sedis
8999	Scymnosaurus sp.	Lycosuchidae
		incertae sedis
9005	Scymnosaurus major	nomen dubium
		Lycosuchidae
		incertae sedis
9012a	Ptomalestes avidus	lost
9015	Pristerognathus sp.	Gorgonopsia
9083	Pristerosaurus microdon	nomen dubium
		Scylacosauridae
		incertae sedis
9084	Scymnosaurus ferox	Lycosuchidae
		incertae sedis
9084a	Pristerognathus sp.	Pardosuchus
		whaitsi.
		See also
		description of two
		additional
		snouts, one centrum
		and one humerus

		included with the specimen.
9088a	Cynariognathus sp.	Early Theocephalia incertae sedis
9111	Pristerognathus sp.	Pardosuchus whaitsi
9112	Alopecognathus angusticeps	Glanosuchus macrops
9126	Scymnosaurus sp.	Theriodontia incertae sedis
9342	Alopecognathus angustioriceps	Glanosuchus macrops
9356a	Pristerognathoides roggeveldensis	Glanosuchus macrops
10556	Scymnosaurus major	Lycosuchidae incertae sedis
11456	Pristerognathus sp.	Glanosuchus macrops
11459	Scymnosaurus sp.	Early Therocephalia incertae sedis
11460	Ptomalestes avidus	Glanosuchus macrops
11560a	Cynariognathus paucioridens	Scyalcosauridae incertae sedis
11586	Cynariognathus paucioridens	Scylacosauridae incertae sedis See also same number as Pristerognathus sp.
11689	Pristerognathoides vanwyki	Scylacosauridae incertae sedis
11833	Scymnosaurus sp.	Early Therocephalia incertae sedis
11842	Pristerognathus sp.	Early Therocephalia incertae sedis
11843	Glanosuchus macrops	VALID
11848	Pristerognathus sp.	Pristerognathus polyodon
11871	Pristerognathus sp.	Glanosuchus macrops
11872	Pristerognathus sp.	Scylacosauridae incertae sedis
11873	Pristerognathus sp.	Scylacosauridae incertae sedis
11874	Pristerognathus sp.	Glanosuchus macrops
11875	Pristerognathus sp.	?ictidorhinid
11876	Pristerognathus sp.	Glanosuchus macrops
11888	Therioides cyniscus	Scylacosaurus sclateri
11891	Pristerognathoides minor	Scylacosauridae incertae sedis
11893	Pristerognathoides vanwyki	Glanosuchus macrops
11936	Pristerognathus sp.	Lycosuchidae incertae sedis
11942	Ptomalestes avidus	Pristerognathus polyodon
11944	Maraisaurus parvus	See Pristerognathoides parvus
11956	Pristerognathus sp.	?ictidorhinid
11957	Pristerognathus sp.	Ictidosaurus angusticeps
11960	Pristerognathus sp.	Scylacosauridae incertae sedis
11961	Scymnosaurus sp.	Lycosuchidae incertae sedis

	11963	Pristerognathus sp.	Glanosuchus macrops
	11964	Glanosuchus macrops	VALID
	11965	Pristerognathus sp.	Theriodontia incertae sedis
	11966	Pristerognathus sp.	lost
	11967	Pristerognathus sp.	Glanosuchus macrops
	11968	Cynariognathus sp.	Glanosuchus macrops
	12185	Zinnosaurus paucidens	Lycosuchus vanderrieti
TM			
	254	Hofmeyria atavus	Hofmeyriidae
	266	Cynariognathus gallowayi	Glanosuchus macrops
	272	Notaelurodon kitchingi	Advanced therocephalian
	275	Trochorhinus vanhoepeni	nomen dubium Lycosuchidae incertae sedis
	1491	Alopecognathus megalops	nomen dubium Scylacosauridae incertae sedis
UCMP			
	40467	Mirotenthes digitipes	Hofmeyriidae
UM			
	1934 VIII 30	Cynariognathus seeleyi	nomen dubium Scylacosauridae incertae sedis
	1936 II 9	Pristerognathoides peyeri	Glanosuchus macrops
US			
	D173	Lycosuchus vanderrieti	VALID

11. ABBREVIATIONS

ac	anterior canine
aca	anterior canine alveolus
ad	angle of dentary
adp	anterodorsal process of prootic
ae	anterior process of epipterygoid
af	alveolar foramen
aj	anterior process of jugal
alr	anterior lacrimal ridge
amf	anterior maxillary fossa
AMNH	American Museum of Natural History
an	angular
ano	angular notch
ap	apical foramina
apc	anterior process of coronoid
ape	anterior process of ectopterygoid
apf	anterior premaxillary foramen
apl	anterior process of lacrimal
apn	anterodorsal process of nasal
apr	anterior pterygoid ramus
aps	anterodorsal process of supraoccipital
ar	anterior ridge of angular
arp	articular pit
art	articular
asf	anterior septomaxillary foramen

avp anteroventral process of prootic

BMNH British Museum of Natural History, London

bo basioccipital

BPIP Bernard Price Institute for Palaeontology, Johannesburg

bpt basipterygoid process

bs basisphenoid

bsk basisphenoid keel

bt basal tuber

c canine

cape contact of anterior process of epipterygoid

cb canine boss

cc crista choanalis

ce cavum epipterygoidum

ci cancellous infilling of canine alveolus

cmn canal for maxillary nerve

co coronoid

cop coronoid process of dentary

cp cultriform process

d dentary

d1 angular depression between dorsal and anterior ridges

d2 angular depression between anterior and anteroventral ridges

d3 angular depression between anteroventral and ventral ridges

d4 angular depression between ventral and posterior ridges

dcv dorsal crest of vomer

dfp dorsal foramen of premaxilla

di diastema

dj dorsal process of jugal

dl dorsal lamina of vomer

dlp dorsal lamina of pterygoid

dp dorsal process of prootic

dpc dorsal process of coronoid

dpe dorsal process of ectopterygoid

dps dorsal process of stapes

ds dorsum sellae

dso dorsal process of opisthotic

dsq dorsal process of squamosal

ect ectopterygoid

en external naris

eo exoccipital

ept epipterygoid

f frontal

fa fossa between mastoid and quadrate heads of paroccipital process

fc functional canine

ff foramen for facial nerve

fic foramen for internal carotid

fl foramen of lacrimal canal

FMNH Field Museum of Natural History, Chicago

fm foramen magnum

fo fenestra ovalis

fos	fossa on surangular
fp	fossa on postorbital
fs	footplate of septomaxilla
fv	footplate of vomer
gl	glenoid
GS	Geological Survey of South Africa, Pretoria
i	incisor
ic	choana
ip	incisura prootica
irc	impression of replacement canine
is	intermediate process of squamosal
iv	interpterygoid vacuity
j	jugal
l	lacrimal
lc	lower canine
lcq	lateral condyle of quadrate
ler	lacrimo-ectopterygoidal ridge
li	lower incisor
lmr	lateral maxillary ridge
lpb	lateral process of basioccipital
lpp	lateral process of prootic
lpr	lacrimo-palatine ridge
lpf	lateral process of frontal
lrq	lateral ridge of quadrate
lsq	lateral process of squamosal
m	maxilla
man	maxillary antrum

mc	meckelian canal
mcq	medial condyle of quadrate
me	mesethmoid
men	mentum
mf	mental foramen
MM	MacGregor Museum, Kimberley
mp	mastoid head of paroccipital
mpa	maxillo-palatine foramen
mpf	maxillo-premaxillary foramen
mpp	maxillary process of premaxilla
mps	medial process of septomaxilla
msf	maxillo-septomaxillary foramen
n	nasal
nc	nuchal crest
nf	nutrient foramen
NM	Natal Museum
np	nasal process of premaxilla
ns	nasal process of septomaxilla
nuf	nuchal fossa
o	orbit
op	opisthotic
ops	otic process of squamosal
os	orbitoshenoid
p	parietal
pa	pila antotica
paf	parietal foramen
pal	palatine

pap	paroccipital process
pas	parasphenoid
pb	pterygoid boss
pbs	parabasisphenoid
pc	postcanine
pca	posterior canine alveolus
pc1	postcanine number one
pc6	postcanine number six
pd	preorbital depression
pdf	postdentary foramen
pe	posterior process of epipterygoid
pf	prefrontal
pfc	previously functional canine
pfo	prefrontal fossa
pfp	posterior foramen of the premaxilla
pg	preorbital groove
pif	pituitary fossa
PIN	Palaeontological Institute Moscow
pj	posterior process of the jugal
pk	parabasisphenoid keel
plp	posterolateral process of palatine
pm	premaxilla
pmf	posterior maxillary fossa
poc	posterior canine
po	postorbital
pof	postfrontal
pp	postparietal

ppf	pterygo-paroccipital foramen
ppfo	posterior palatine foramen
ppp	posterior process of postorbital
ppm	posterolateral process of maxilla
ppq	pterygoid process of quadrate
pqq	position of quadrate and quadratojugal
pra	prearticular
prc	precanine
pro	prootic
ps	posterior process of septomaxilla
psf	posterior septomaxillary foramen
psi	premaxillary sulci
pt	pterygoid
pte	pterygoid teeth
ptf	posttemporal fenestra
ptp	pterygopalatine ridge
ptr	pterygoid ridge
pvc	posteroventral crest of mandible
q	quadrate
qf	quadrate foramen
qj	quadratojugal
qjn	quadratojugal notch
qn	quadrate notch
qp	quadrate head of paroccipital
qqj	quadrate-quadratojugal foramen
qr	quadrate ramus of pterygoid
qs	quadrate process of squamosal

qur quadrate roller

r1 dorsal ridge on reflected lamina

r2 anterior ridge on reflected lamina

r3 anteroventral ridge on reflected lamina

r4 ventral ridge on reflected lamina

r5 posterior ridge on reflected lamina

rc replacement canine

rf reflected lamina of the angular

ri replacement incisor

rp retroarticular process

s stapes

sa surangular

SAM South African Museum

sc sagittal crest

se sella turcica

ser tooth serrations

sf suborbital fenestra

slc sulcus on lateral surface of coronoid process of dentary

sm septomaxilla

so supraoccipital

sp splenial

spb suture between prootic and basisphenoid

spo ventral suture between prootic and opisthotic

sq squamosal

sqs squamosal sulcus

sr squamosal ridge

ss	squamosal spur
ssa	sulcus for dorsal margin of surangular
sup	sulcus for parietal vein
sym	symphysis
t	tabular
tf	temporal fenestra
TM	Transvaal Museum
tp	transverse process of pterygoid
TN	Type number
tr	tabular ridge
uc	upper canine
UCMP	University of California, Museum of Paleontology
ui	upper incisor
UM	University of Munich
US	University of Stellenbosch
v	vomer
vcp	ventromedian crest of pterygoid
ve	ventral process of ectopterygoid
vep	ventral pterygoparoccipital foramen
vmc	ventromedian crest on vomer
vmf	ventral maxillary flange
vop	vomerine process of premaxilla
vp	ventral process of prootic
vpc	ventral process of coronoid
vpf	ventral premaxillary foramen
vpp	vomerine process of premaxilla
vpr	ventral parietal ridge

za	zygomatic arch
zps	zygomatic process of squamosal

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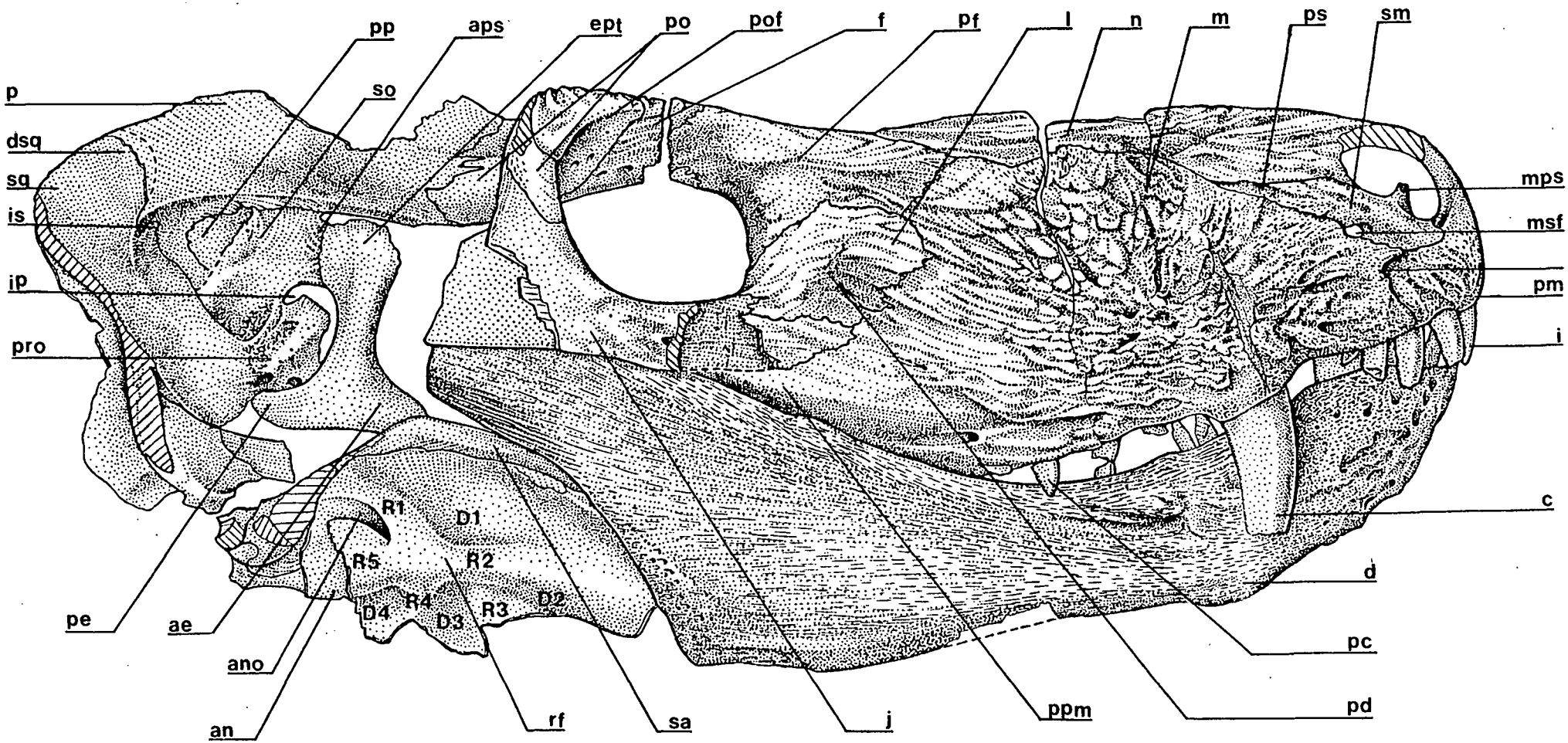

Fig. 1 Right lateral view of the skull of Glanosuchus macrops GS M796 Scale 20 mm.

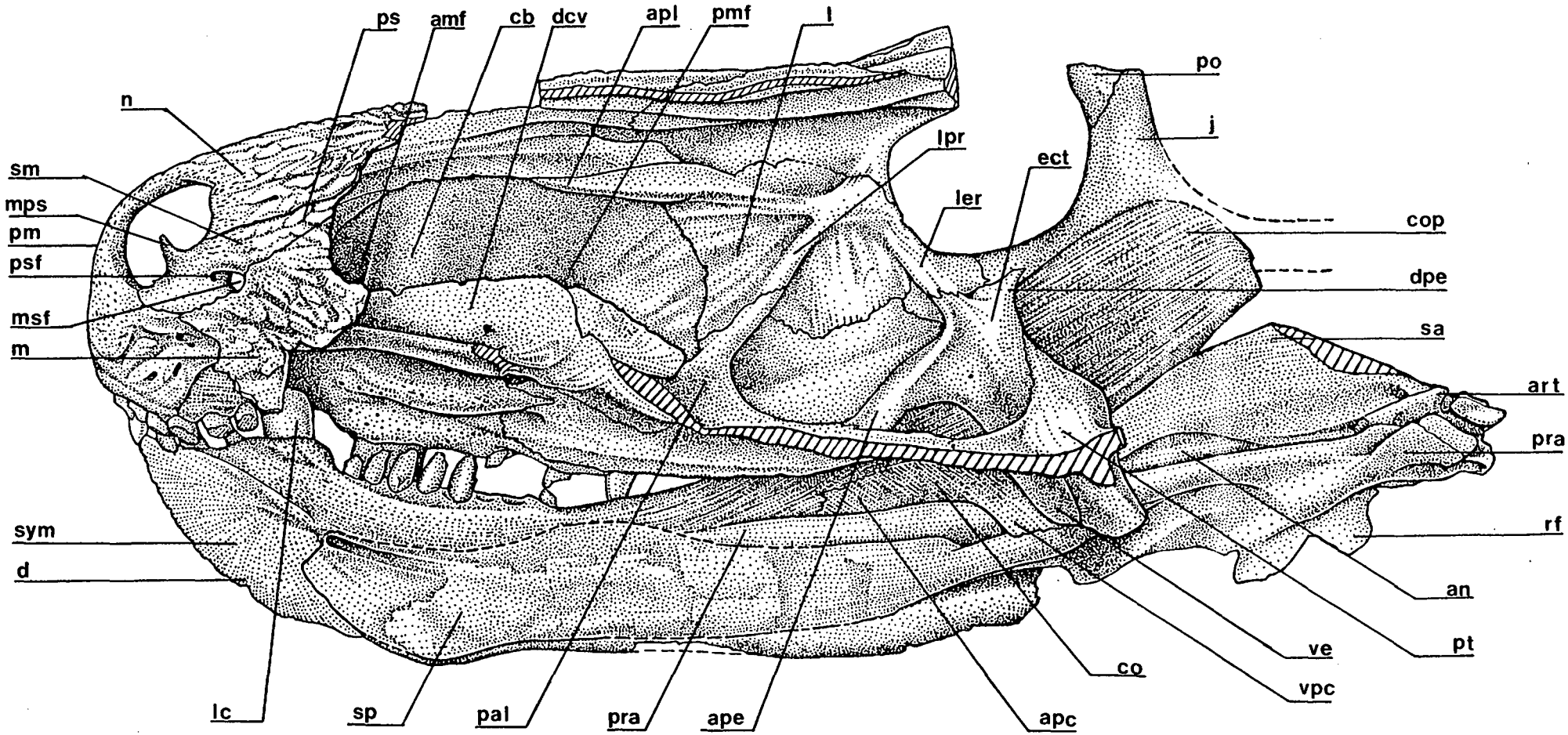

Fig. 2 Medial view of right half of the skull Glanosuchus macrops GS M796 Scale 20 mm.

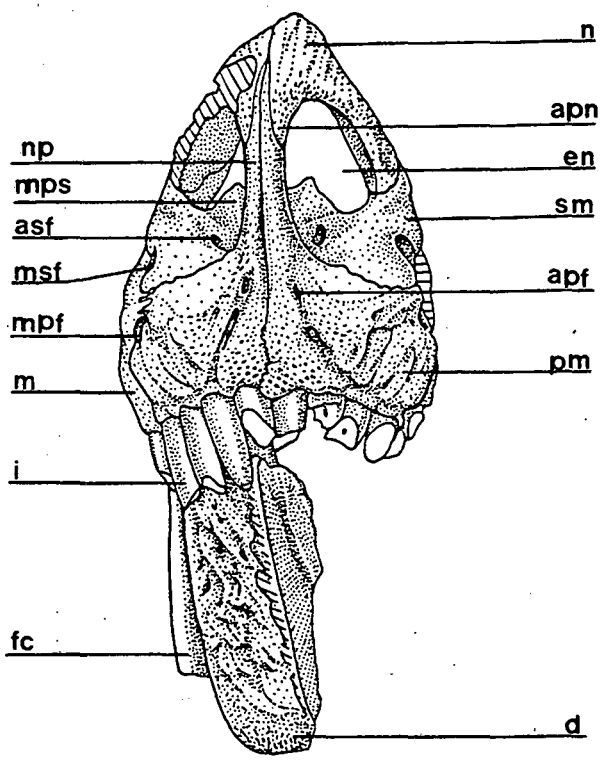

Fig. 3 Anterior view of the snout of *Glanosuchus macrops* GS M796.

Scale 20mm. ⊢——⊣

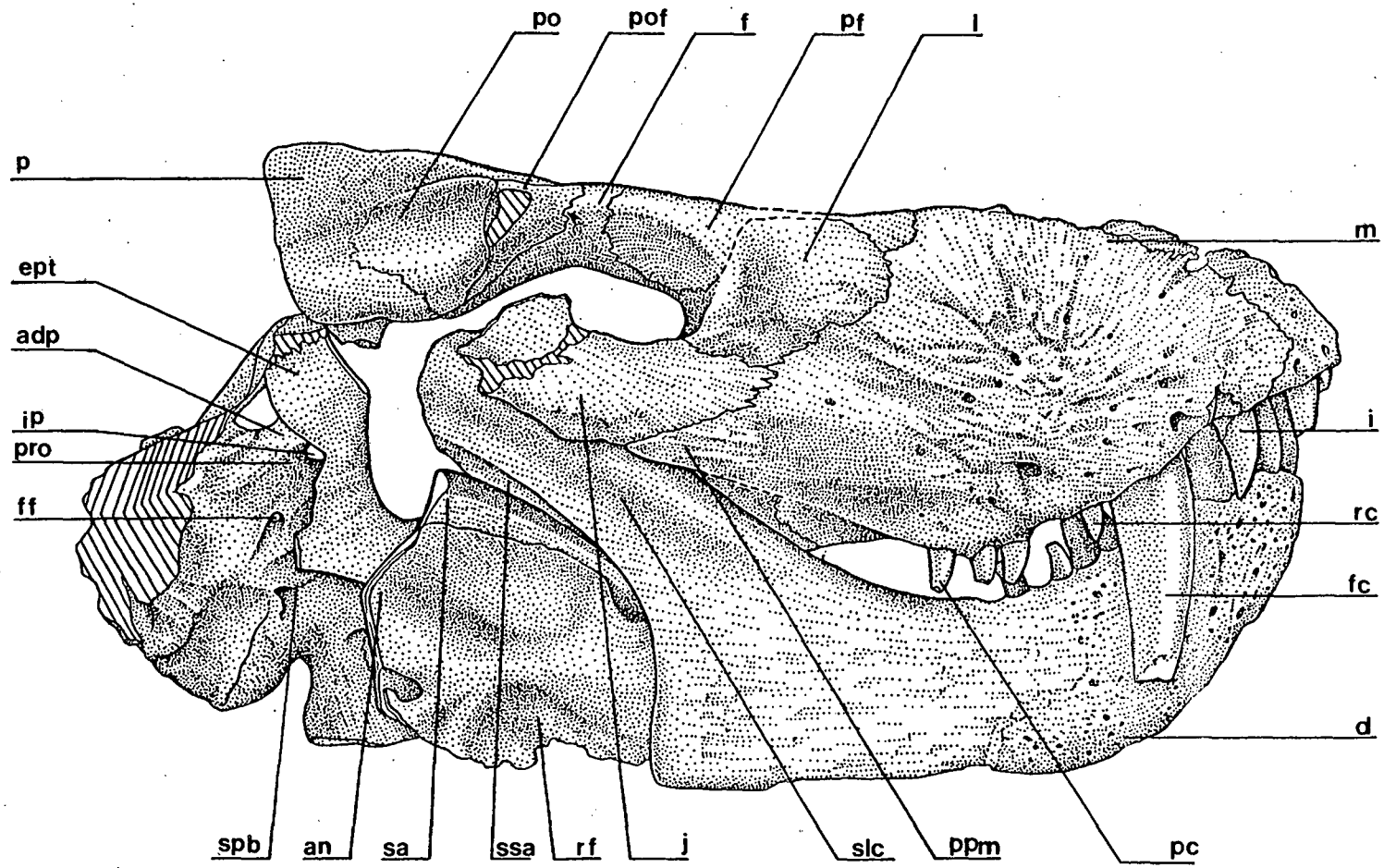

Fig. 4 Right lateral view of the skull of Lycosuchus keyseri GS C60. Scale 20 mm.

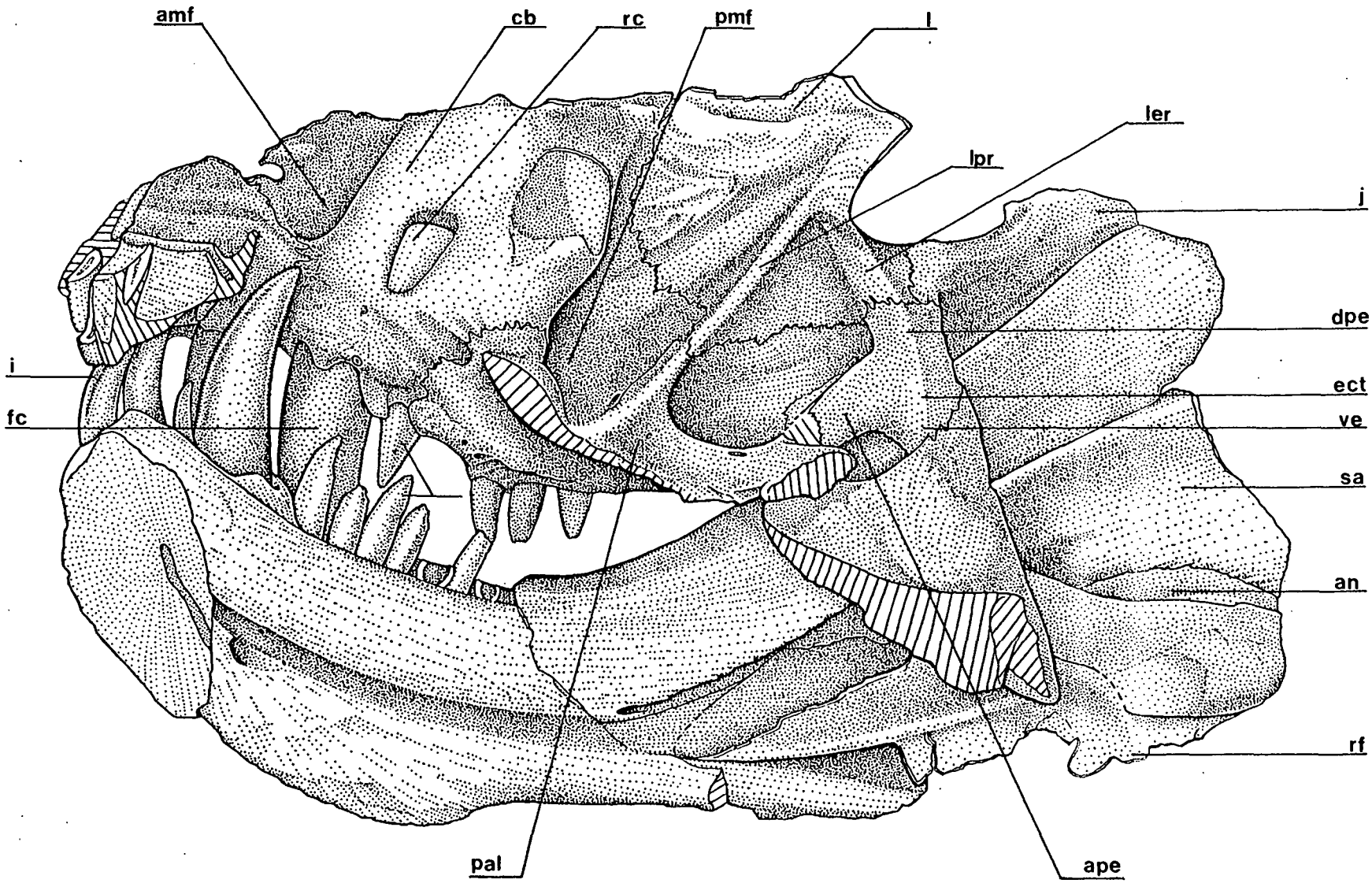

Fig. 5 Medial view of right half of the skull of Lycosuchus keyseri GS C60. Scale 20 mm.

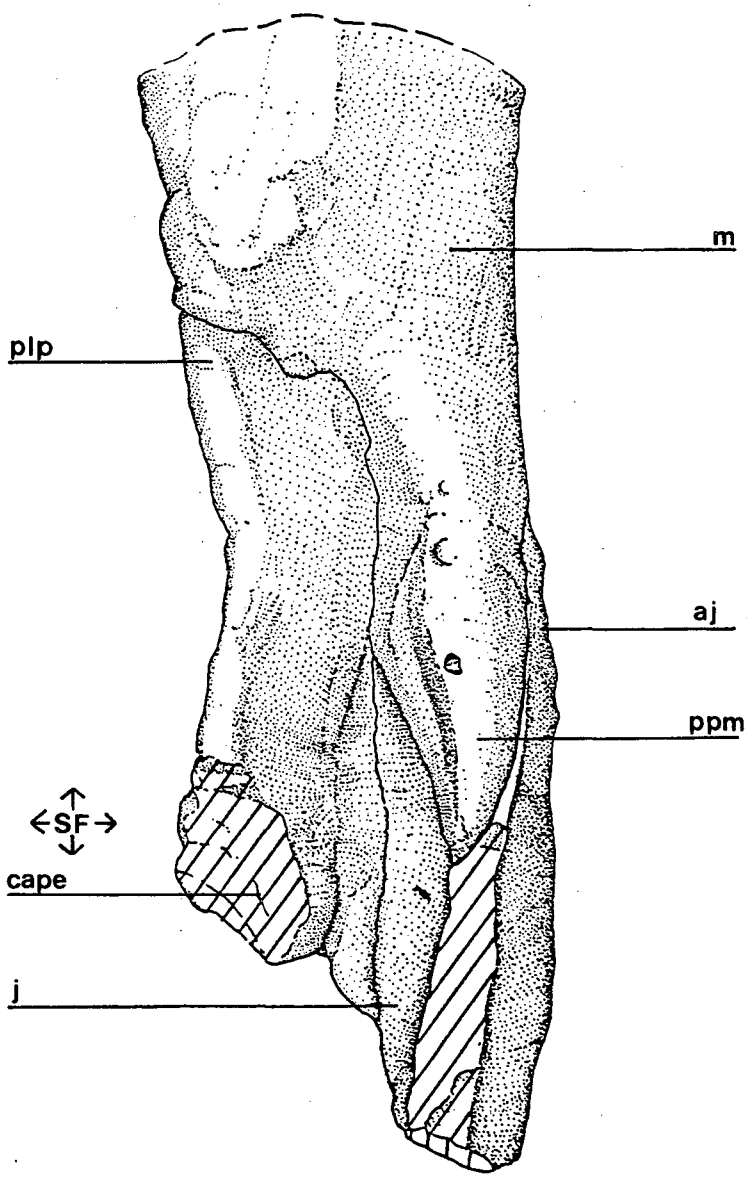

Fig. 6 Ventral view of left maxillo-jugal contact of *Glanosuchus macrops* GS M796. Scale 20mm.

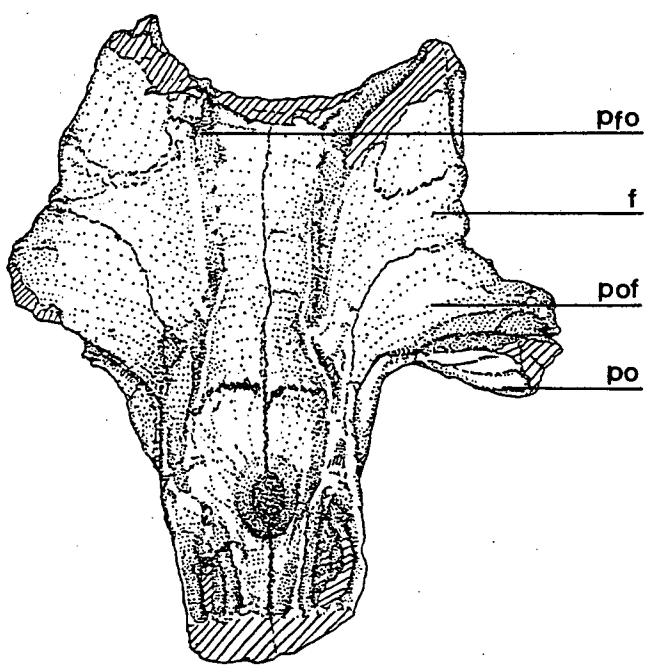

Fig. 7 Ventral view of skull roof of *Lycosuchus keyseri* sp. nov. GS C60.

Scale 20mm. ⊢——⊣

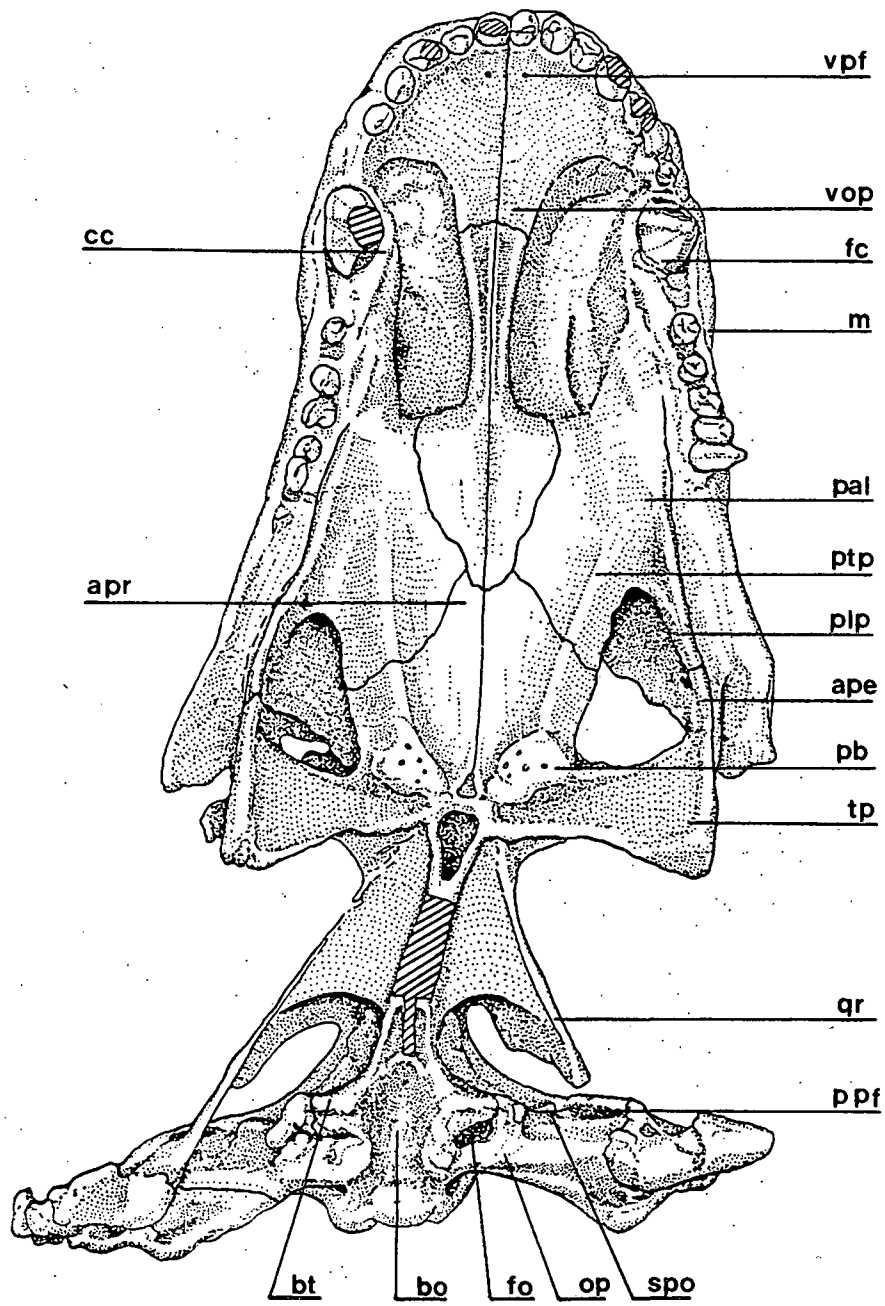

Fig. 8 Ventral view of the type skull of *Ptomalestes avidus* SAM 11942. Scale 20mm.

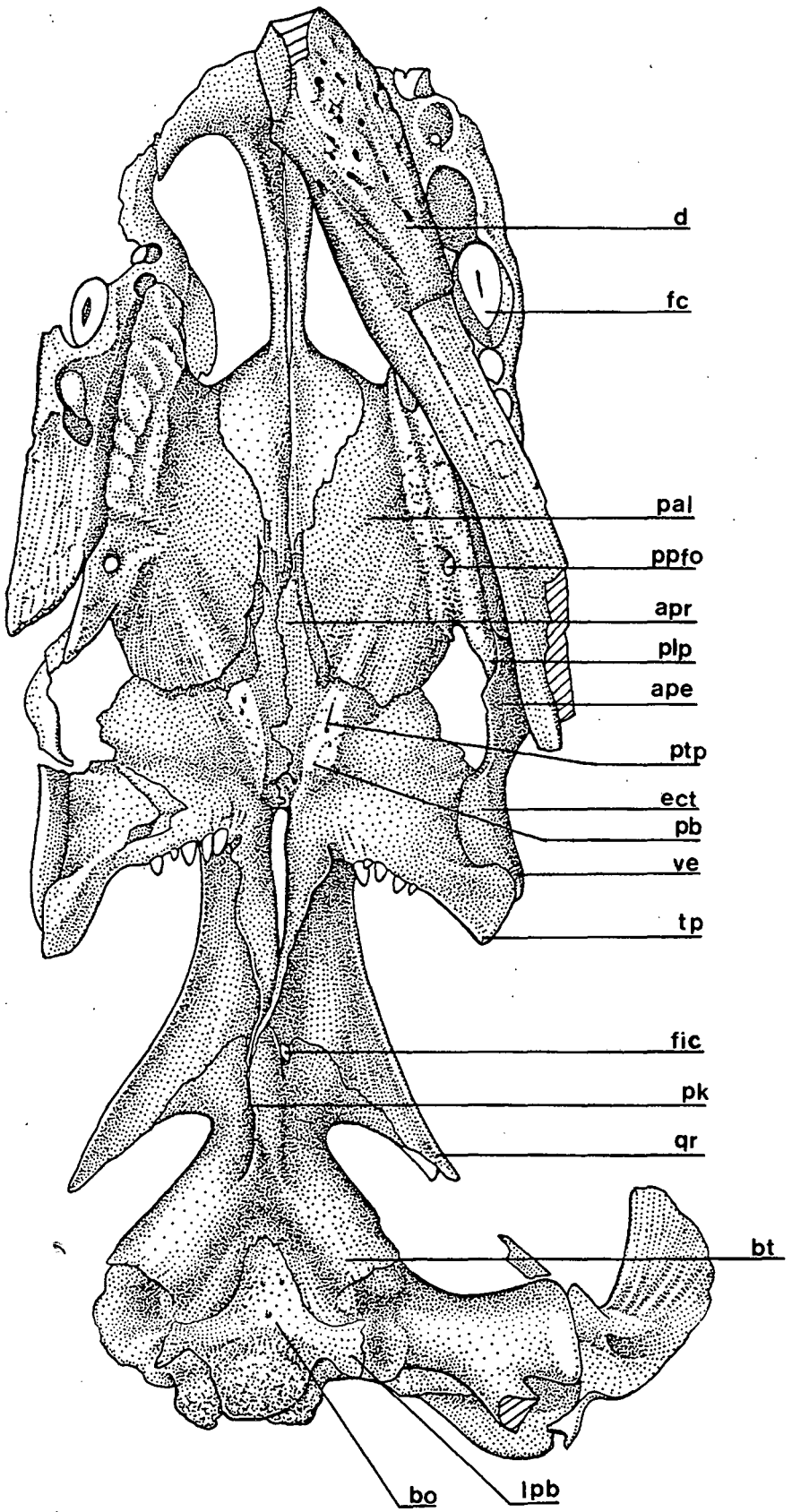

Fig. 9 Ventral view of the skull of *Lycosuchus vanderrieti* GS M793.

Scale 20mm. ⊢——⊣

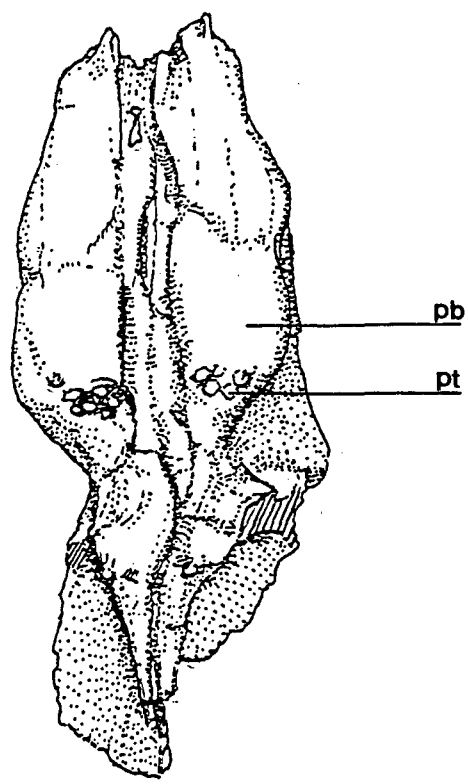

Fig. 10 Ventral view of middle portion of both pterygoids of *Glanosuchus macrops* GS M796. Scale 20mm. ⊢——————⊣

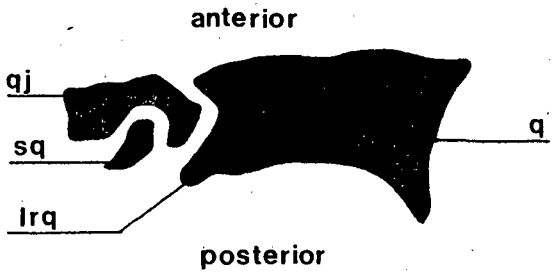

Fig. 11a Horizontal section through quadrate-quadratojugal complex of scylaco-saurid GS RS330 Scale 20 mm.

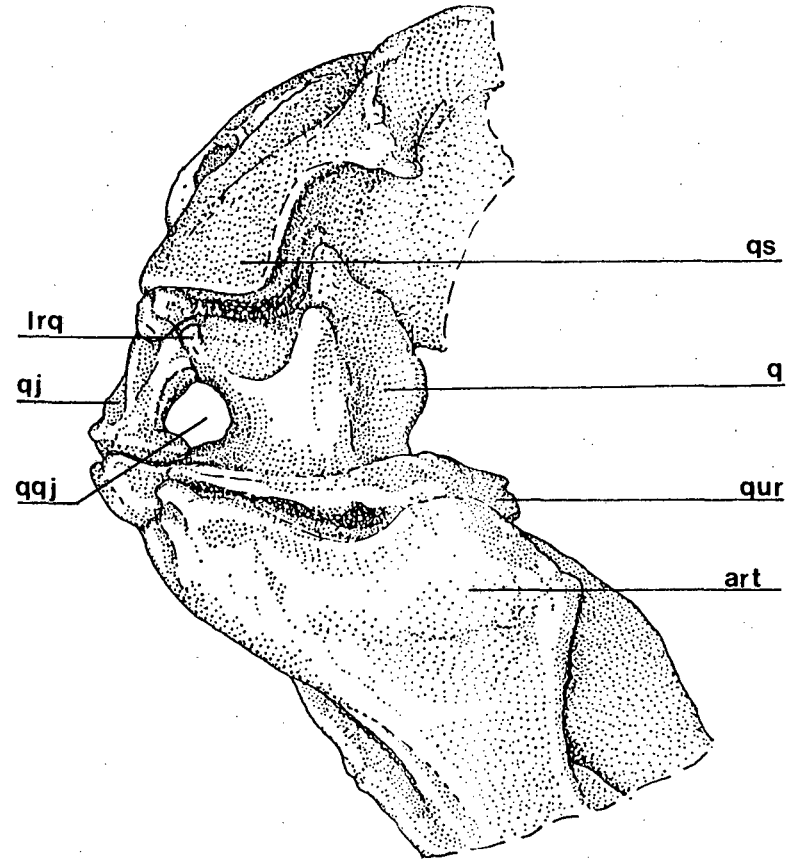

Fig. 11b Partially exploded posteroventral view of suspensorium of scylacosaurid GS RS330 Scale 20 mm.

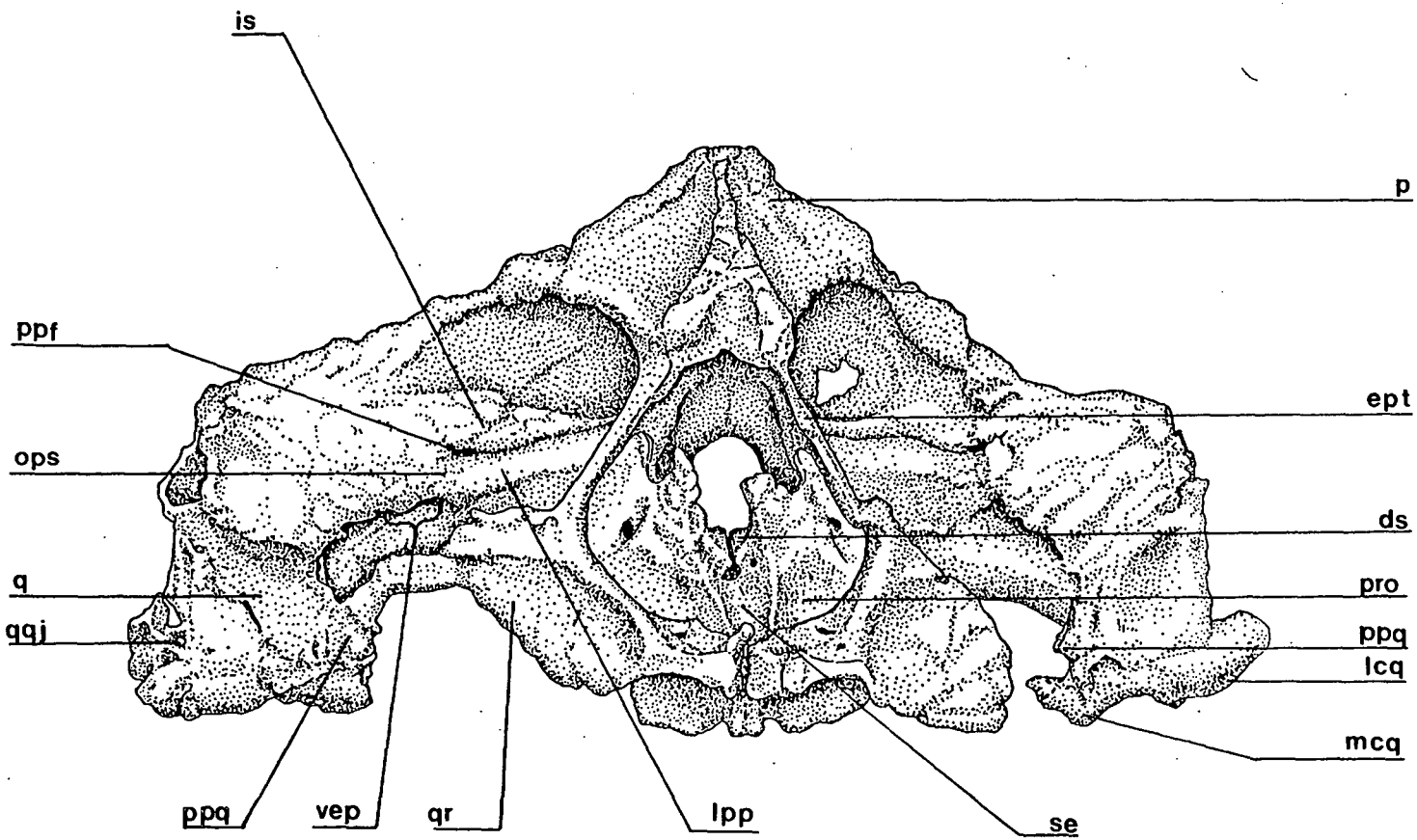

Fig. 12 Anterior view of the braincase and temporal region of the holotype of Ptomalestes avidus SAM 11942. Scale 20 mm.

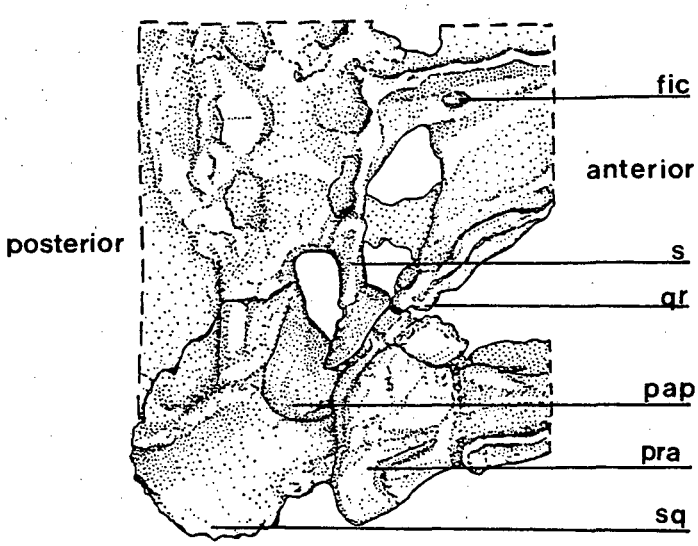

Fig. 13 Ventral view of the skull base and left jaw articulation of an unidentified scylacosaurid GS 273. Scale 20mm. ⊢——⊣

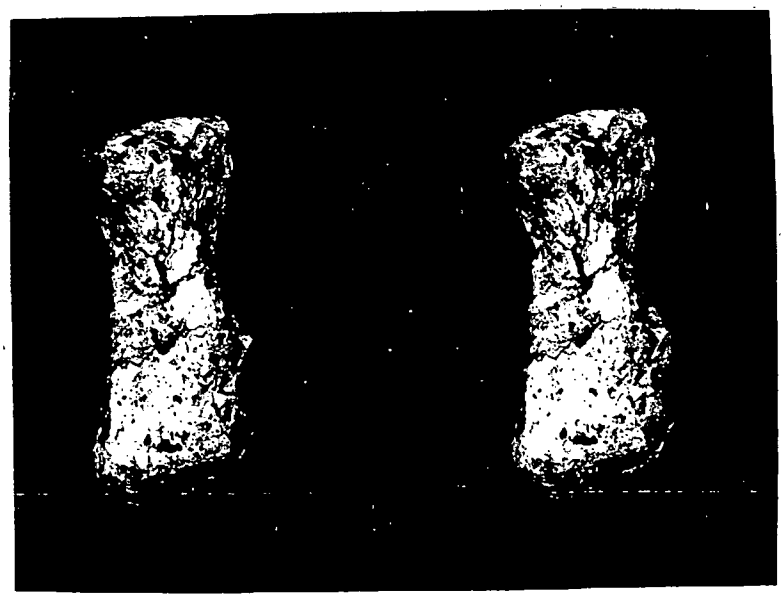

Fig. 14 Stereophotograph of unidentified stapes-like bone associated with the skull of *Glanosuchus macrops* GS M796. Side view 1. Scale 20mm.

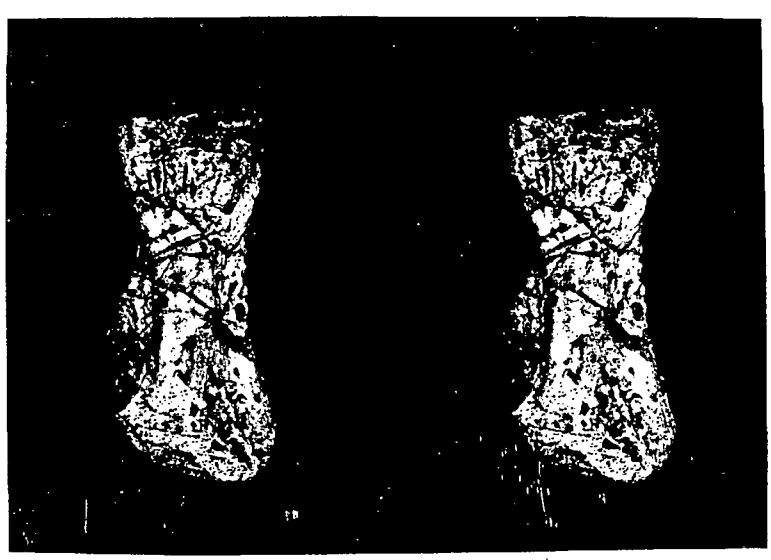

Fig. 15 Stereophotograph of unidentified stapes-like bone associated with the skull of *Glanosuchus macrops* GS M796. Side view 2. Scale 20mm.

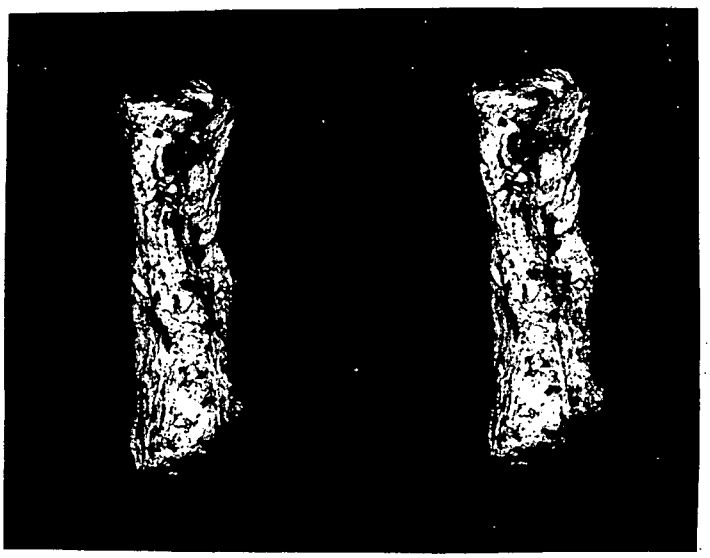

Fig. 16 Stereophotograph of unidentified stapes-like bone associated with the skull of *Glanosuchus macrops* GS M796. Side view 3. Scale 20mm.

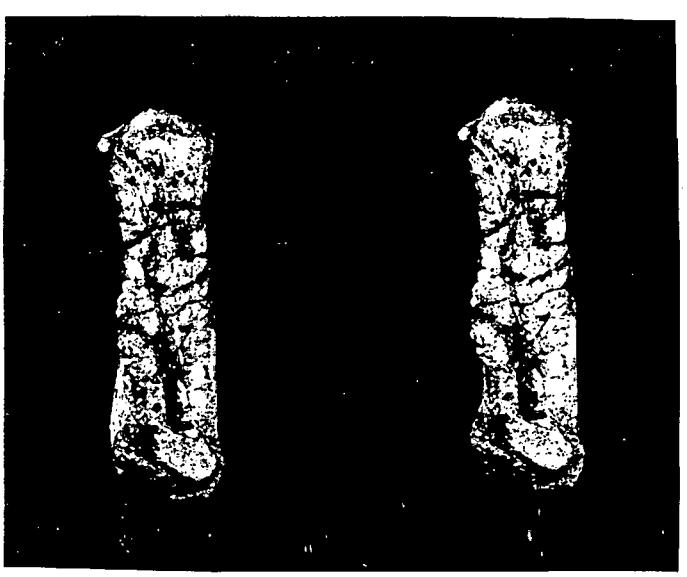

Fig. 17 Stereophotograph of unidentified stapes-like bone associated with the skull of *Glanosuchus macrops* GS M796. Side view 4. Scale 20mm.

Fig. 18 Stereophotograph of unidentified stapes-like bone associated with the skull of *Glanosuchus macrops* GS M796. End view 1. Scale 20mm.

Fig. 19 Stereophotograph of unidentified stapes-like bone associated with the skull of *Glanosuchus macrops* GS M796. End view 2. Scale 20mm.

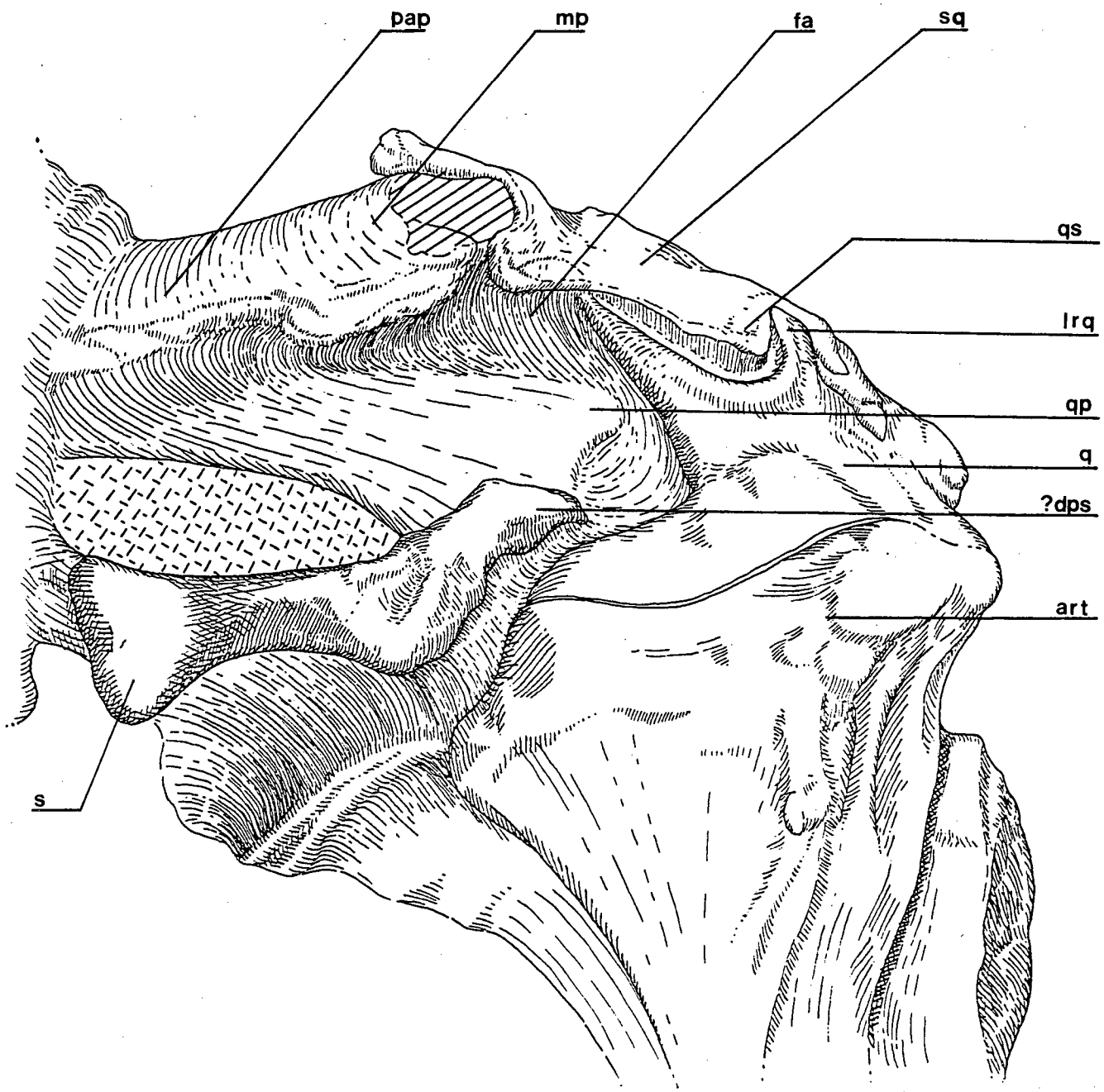

Fig. 20 Posteroventral view of right half of occiput with jaw articulation of *Glanosuchus macrops* GS RS962. Scale 20mm.

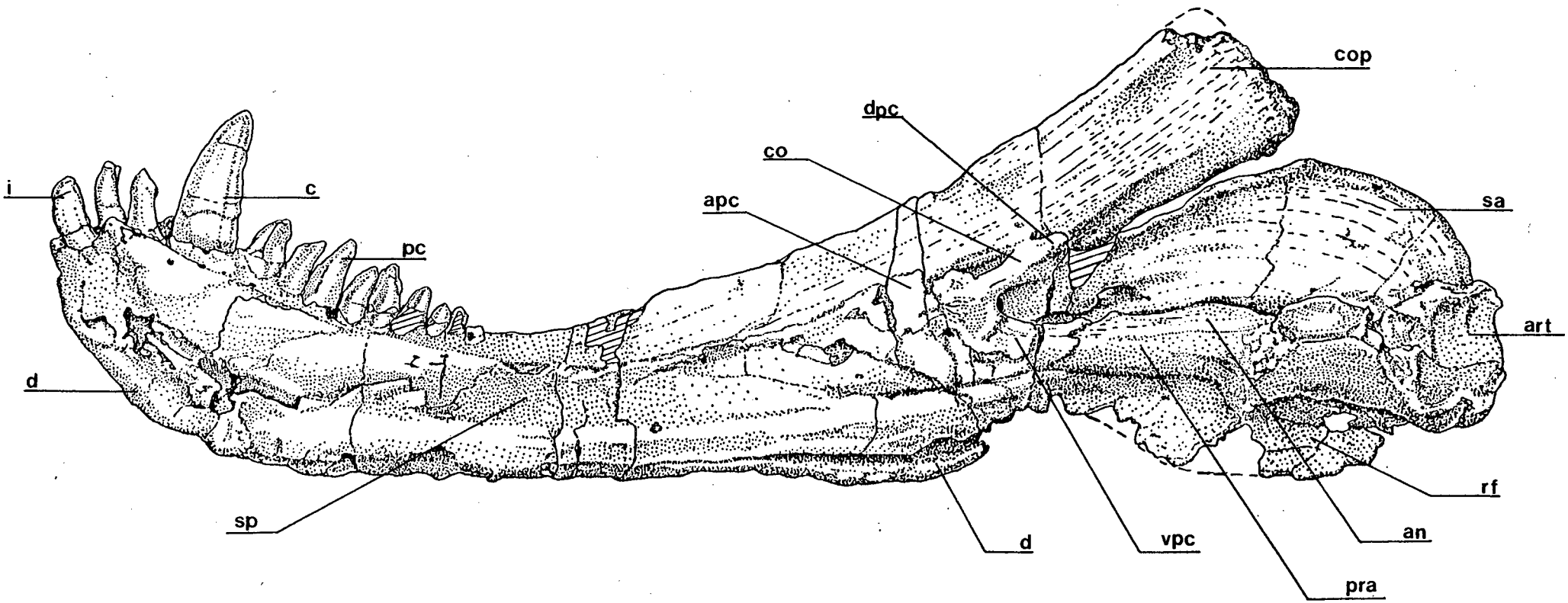

Fig. 21 Medial view of right lower jaw ramus of the holotype Ptomalestes avidus SAM 11942. Scale 20 mm.

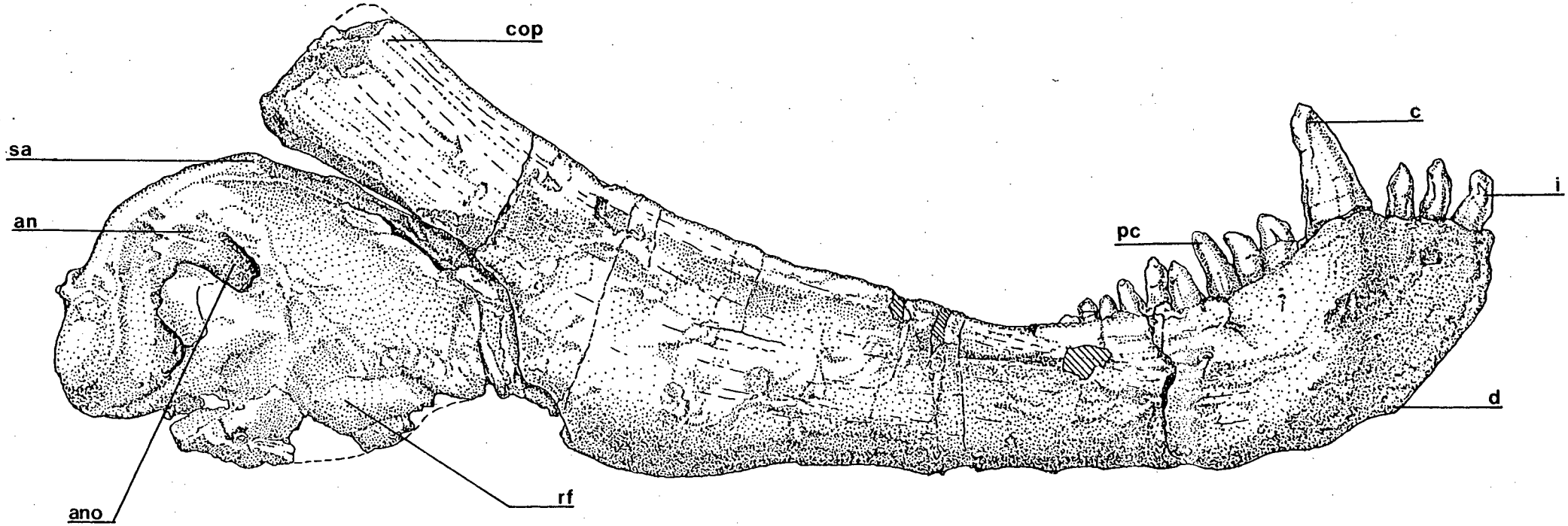

Fig. 22 Lateral view of right lower jaw ramus of the holotype of Ptomalestes avidus SAM 11942. Scale 20 mm.

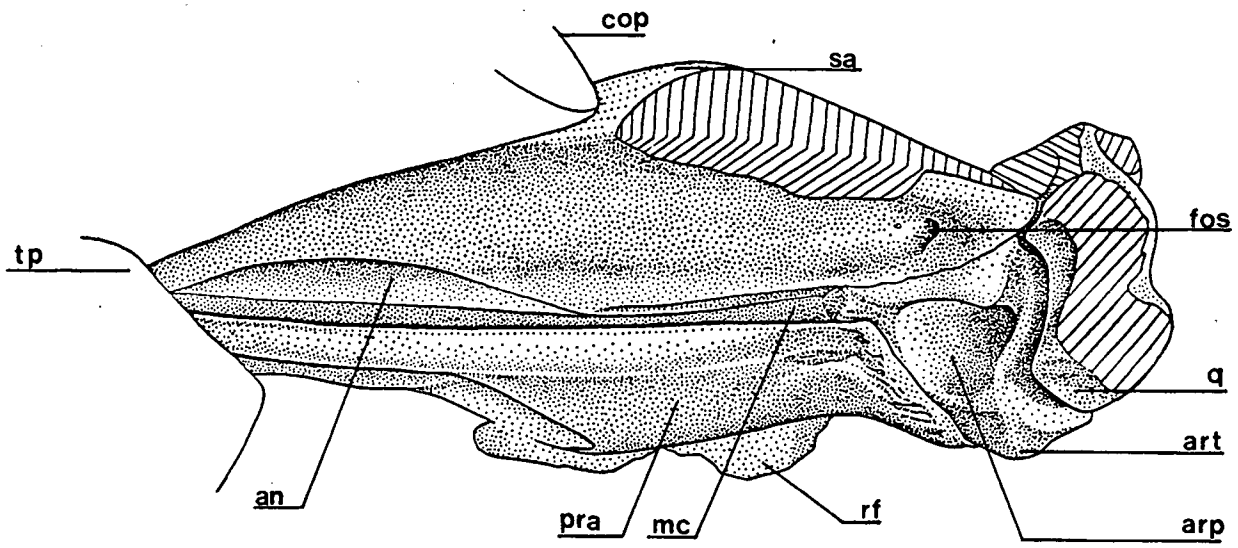

Fig. 23a Dorsal view of postdentary portion of right jaw ramus of *Glanosuchus macrops* GS M796. Scale 20mm.

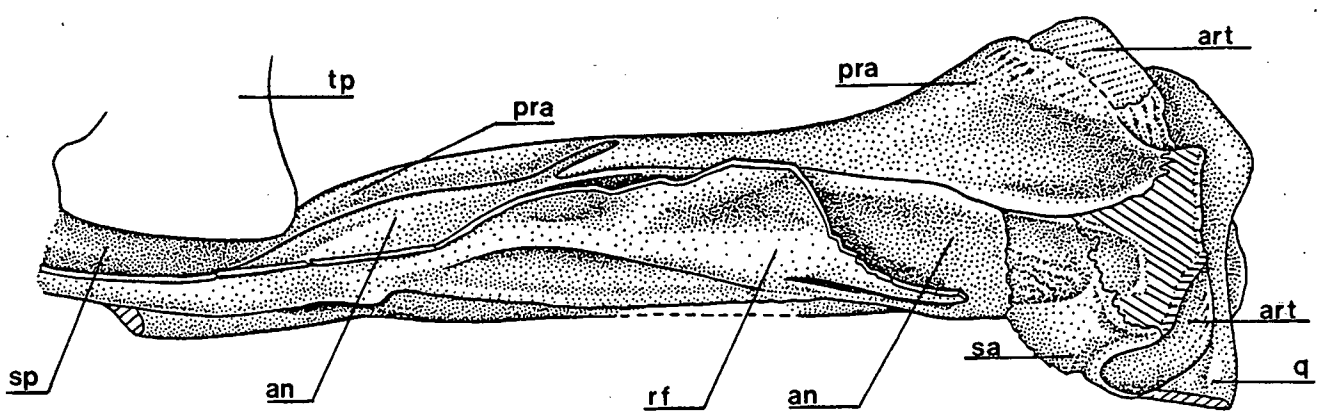

Fig. 23b Ventral view of postdentary portion of right jaw ramus of *Glanosuchus macrops* GS M796. Scale 20mm.

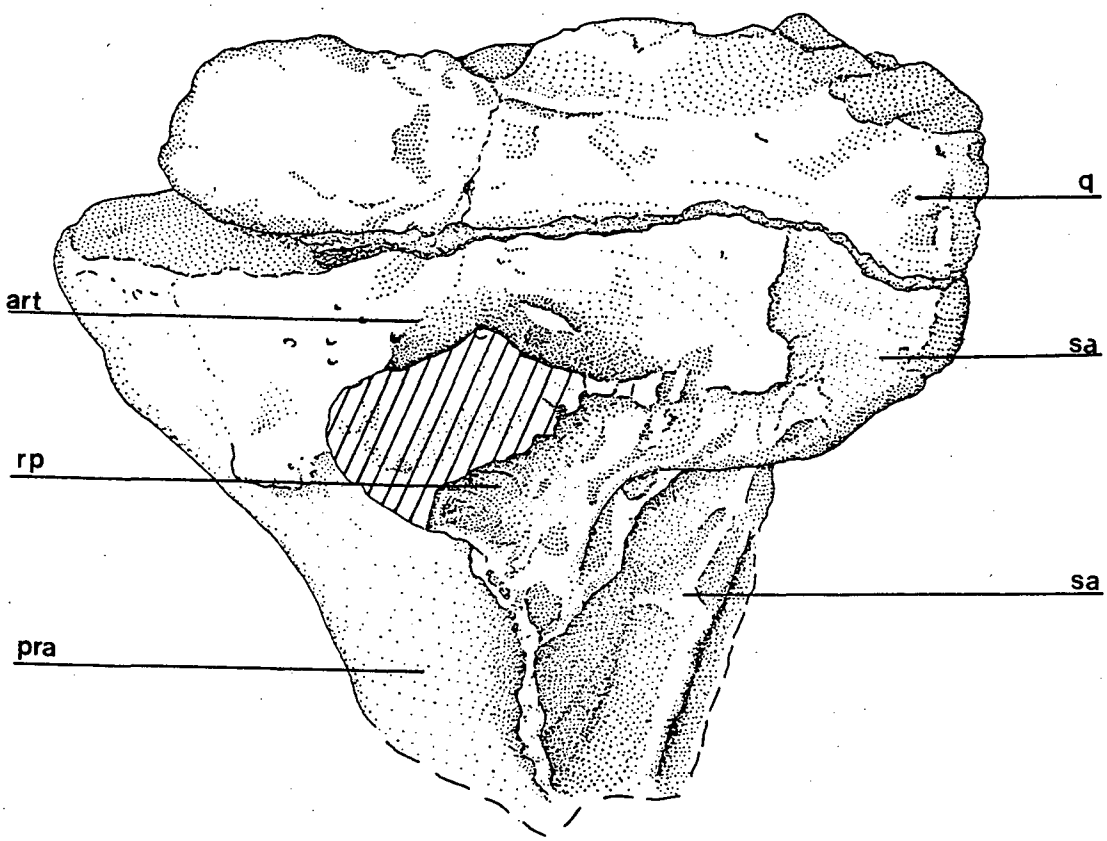

Fig. 24 Posteroventral view of right jaw ramus of *Glanosuchus macrops* GS M796. Scale 20mm.

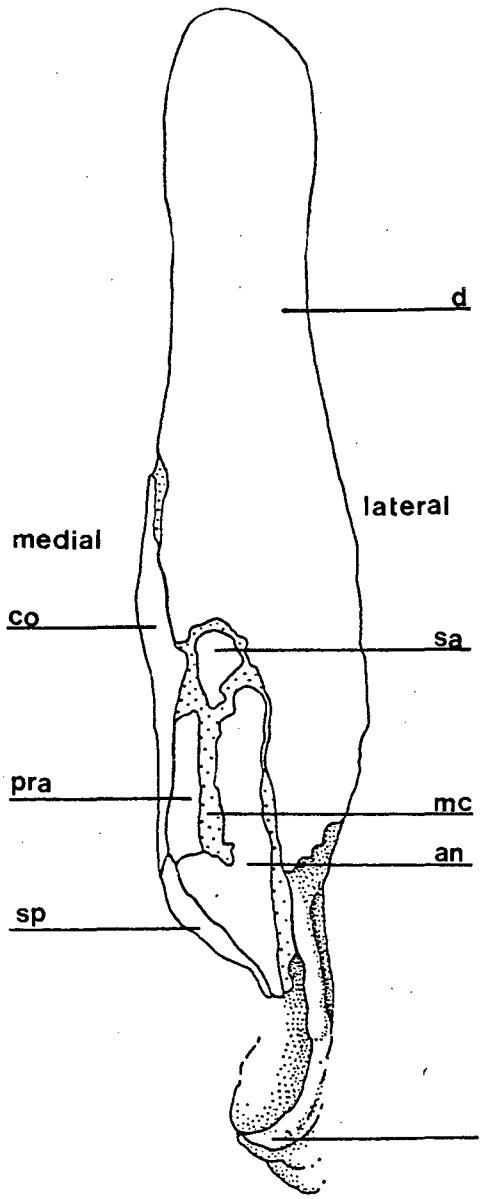

Fig. 25 Transverse section through right jaw ramus of *Glanosuchus macrops* GS M796. Scale 20mm.

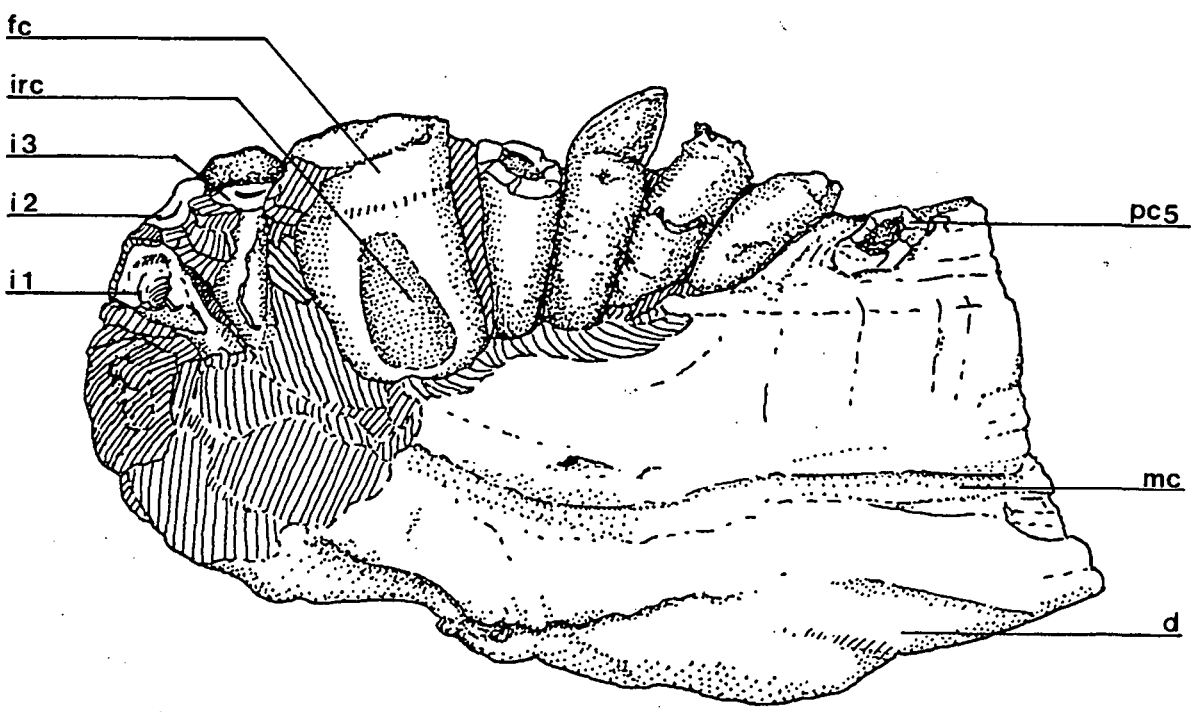

Fig. 26 Medial view of anterior portion of right lower jaw ramus of *Lycosuchus vanderrieti* GS M793. Scale 20mm. ⊢——————⊣

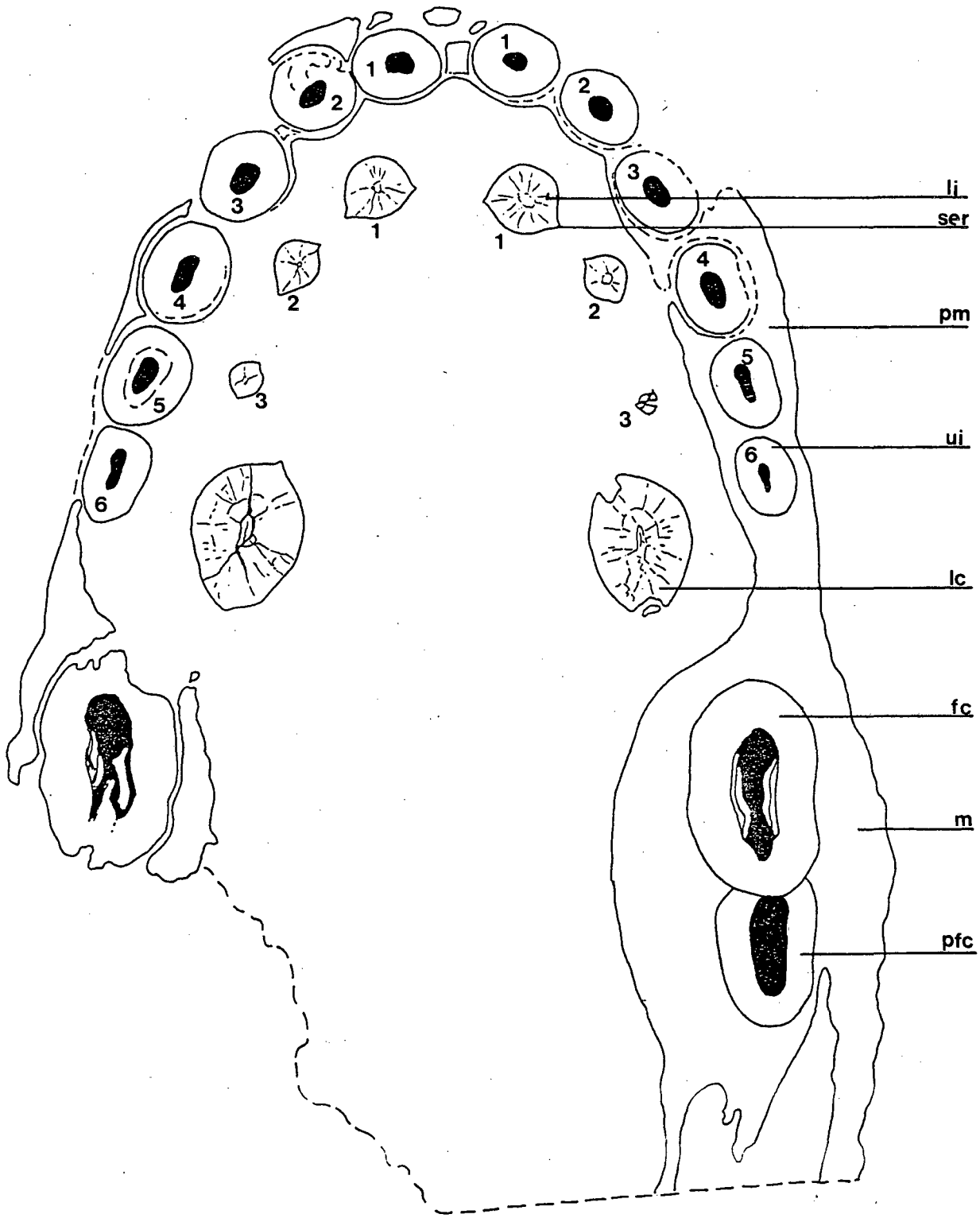

Fig. 27 Horizontal section through the snout of an unidentified scylacosaurid (probably *Glanosuchus*) GS C63. Scale 20mm.

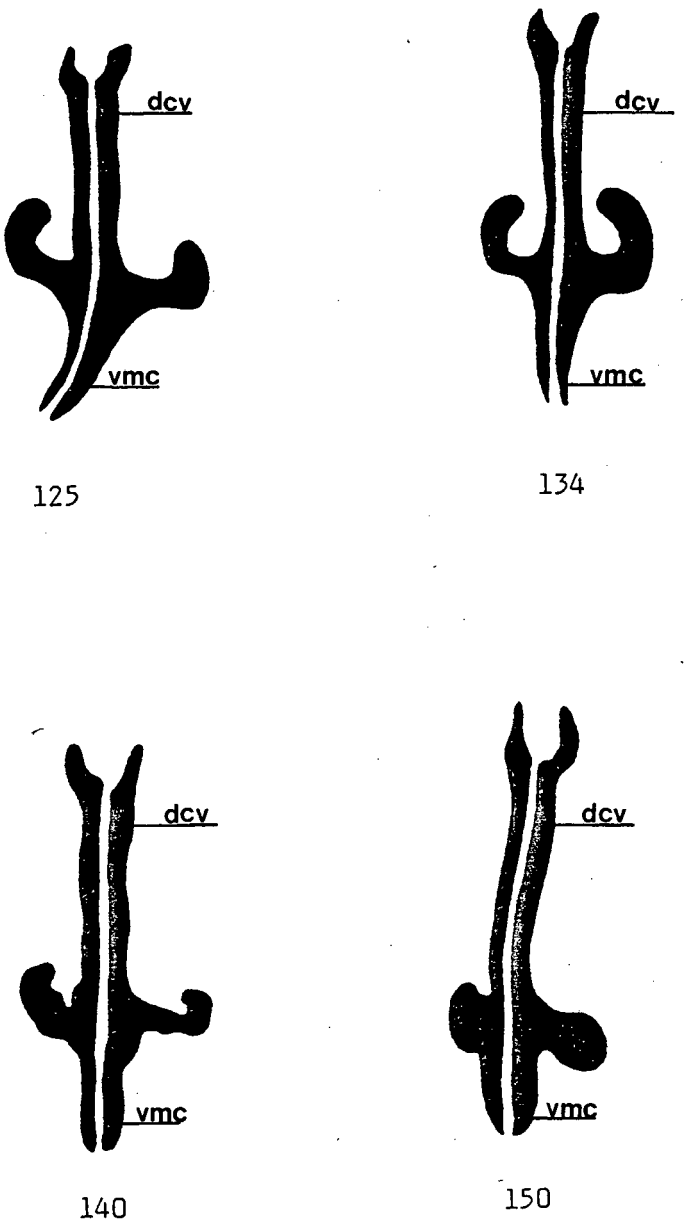

Fig. 28 Four transverse sections through the vomers of a scylacosaurid SAM K238a. Scale 10mm.

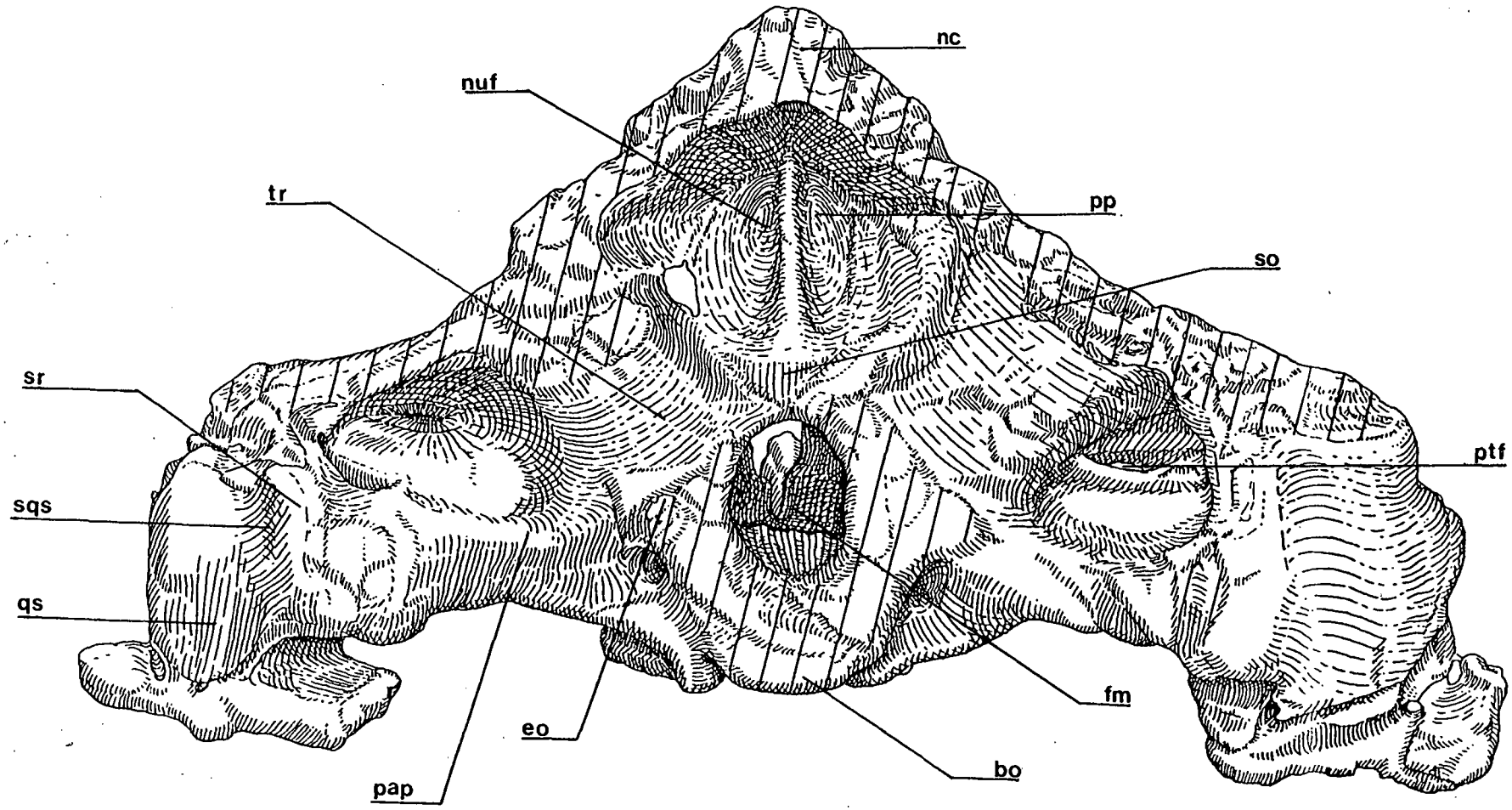

Fig. 29 Occipital view of the holotype of Ptomalestes avidus SAM 11942. Scale 20 mm.

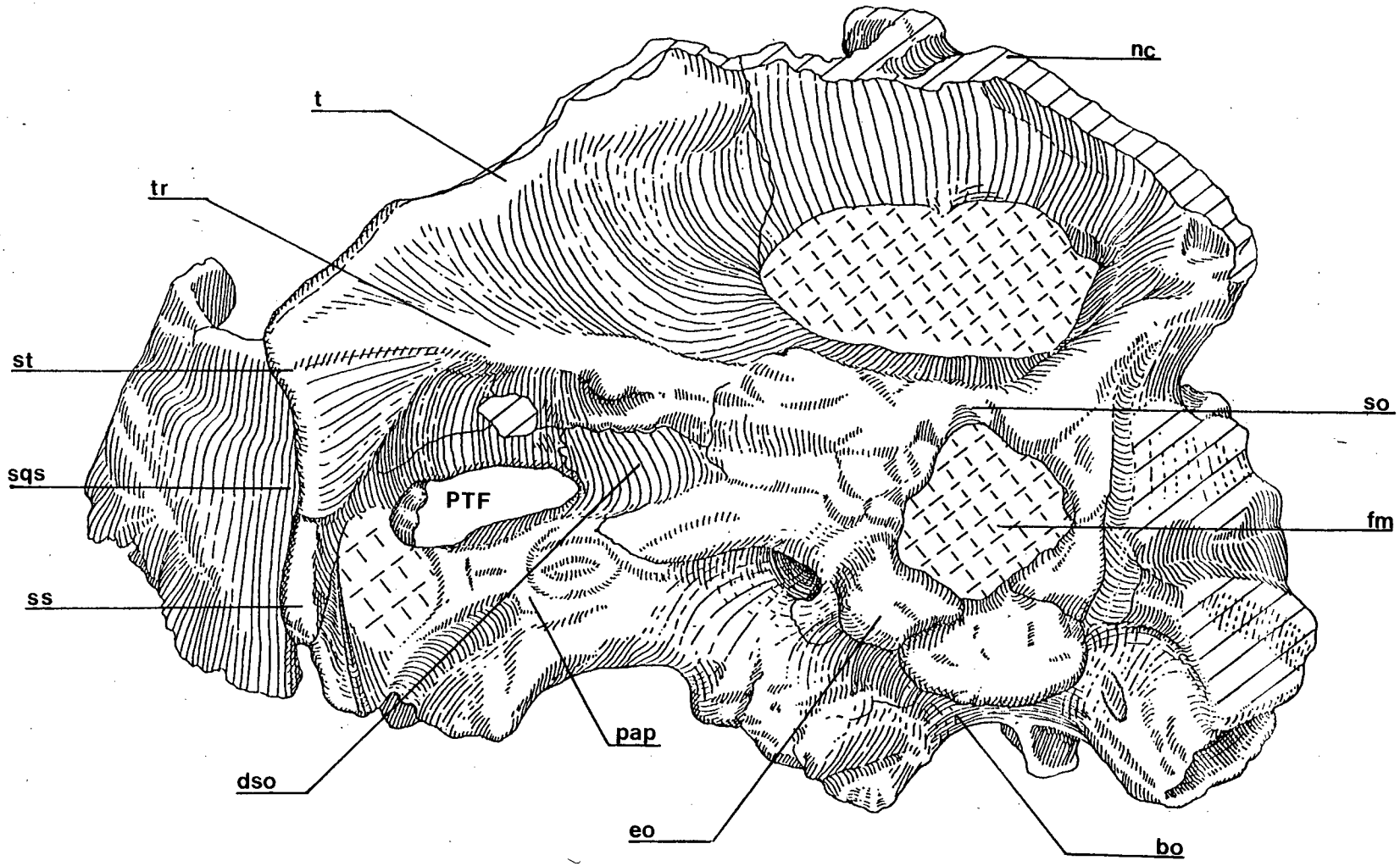

Fig. 30 Occipital view of Lycosuchus vanderrieti GS M793. Scale 20 mm.

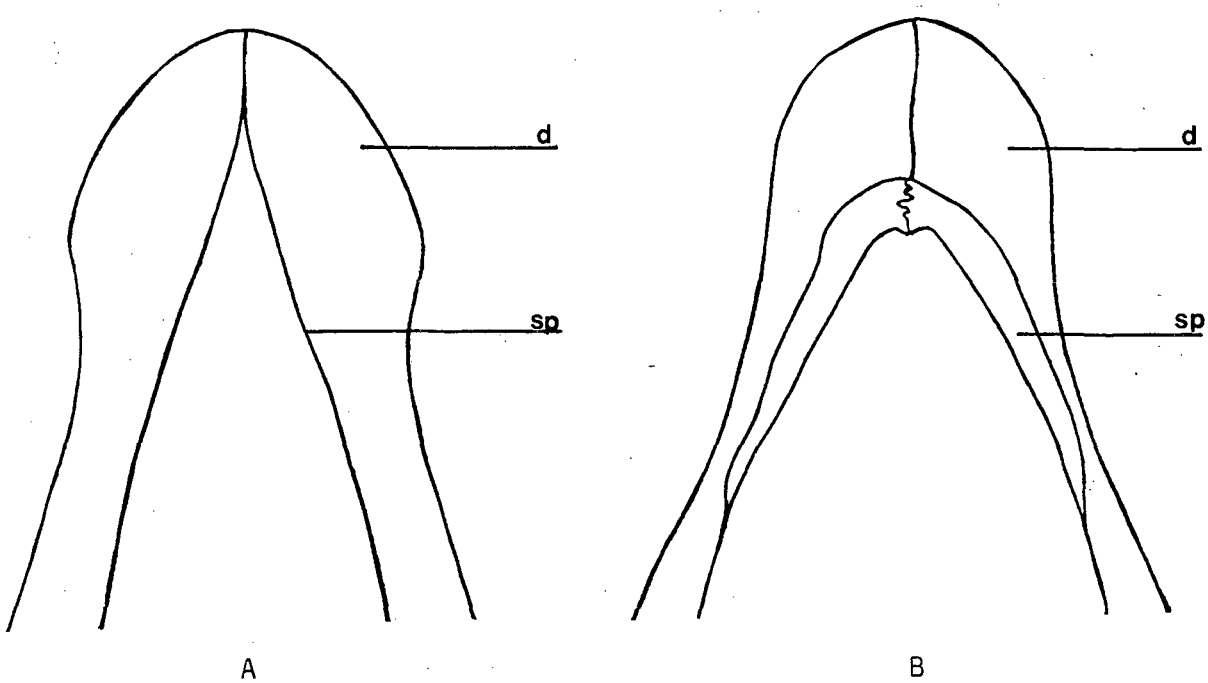

Fig. 31 Diagram illustrating relationship between dentary and splenial in A: Therocephalia, B: Gorgonopsia. Ventral view. No scale.

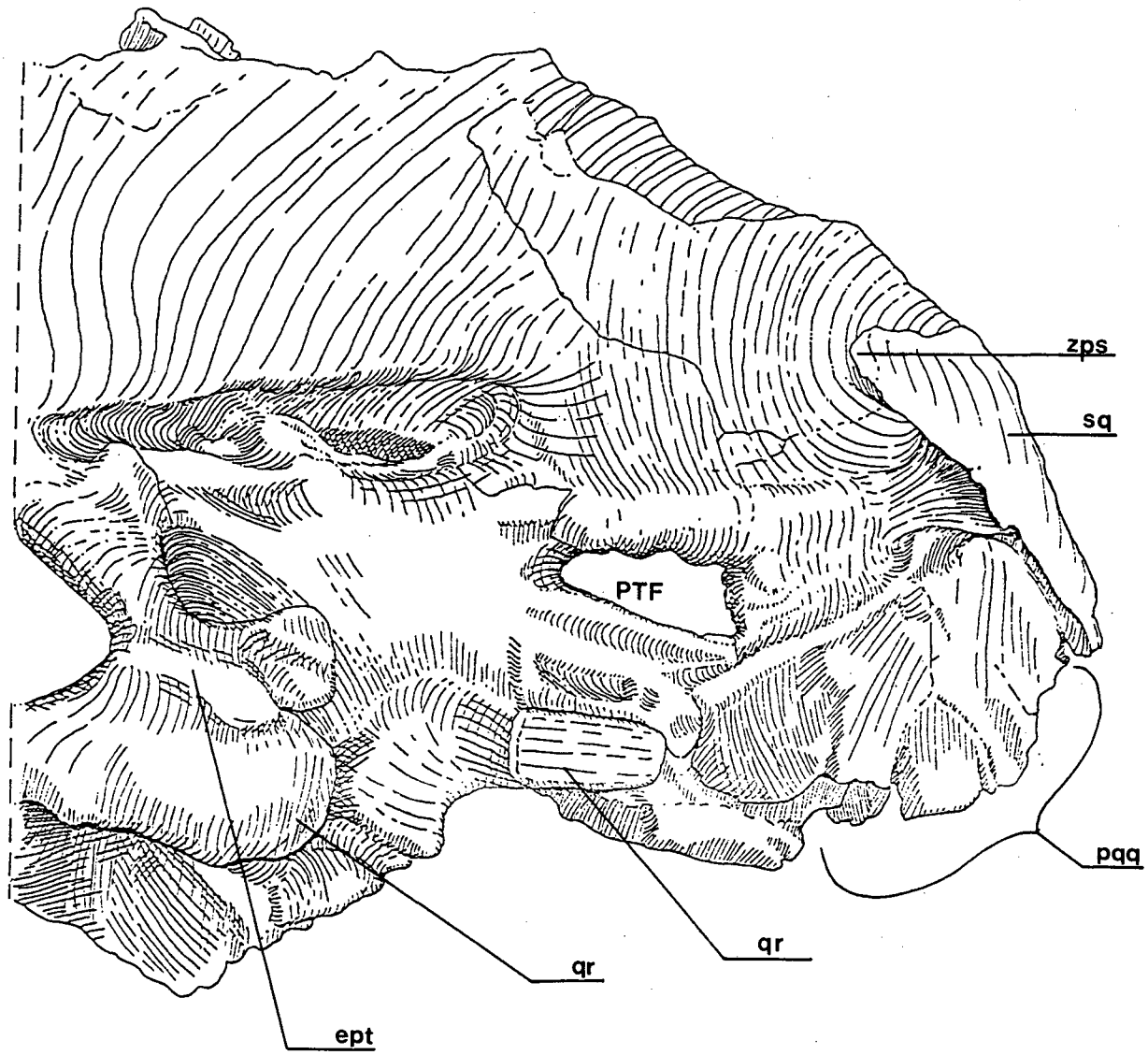

Fig. 32 Anterolateral view of left temporal region in *Lycosuchus vanderrieti* GS M793. Scale 20mm.

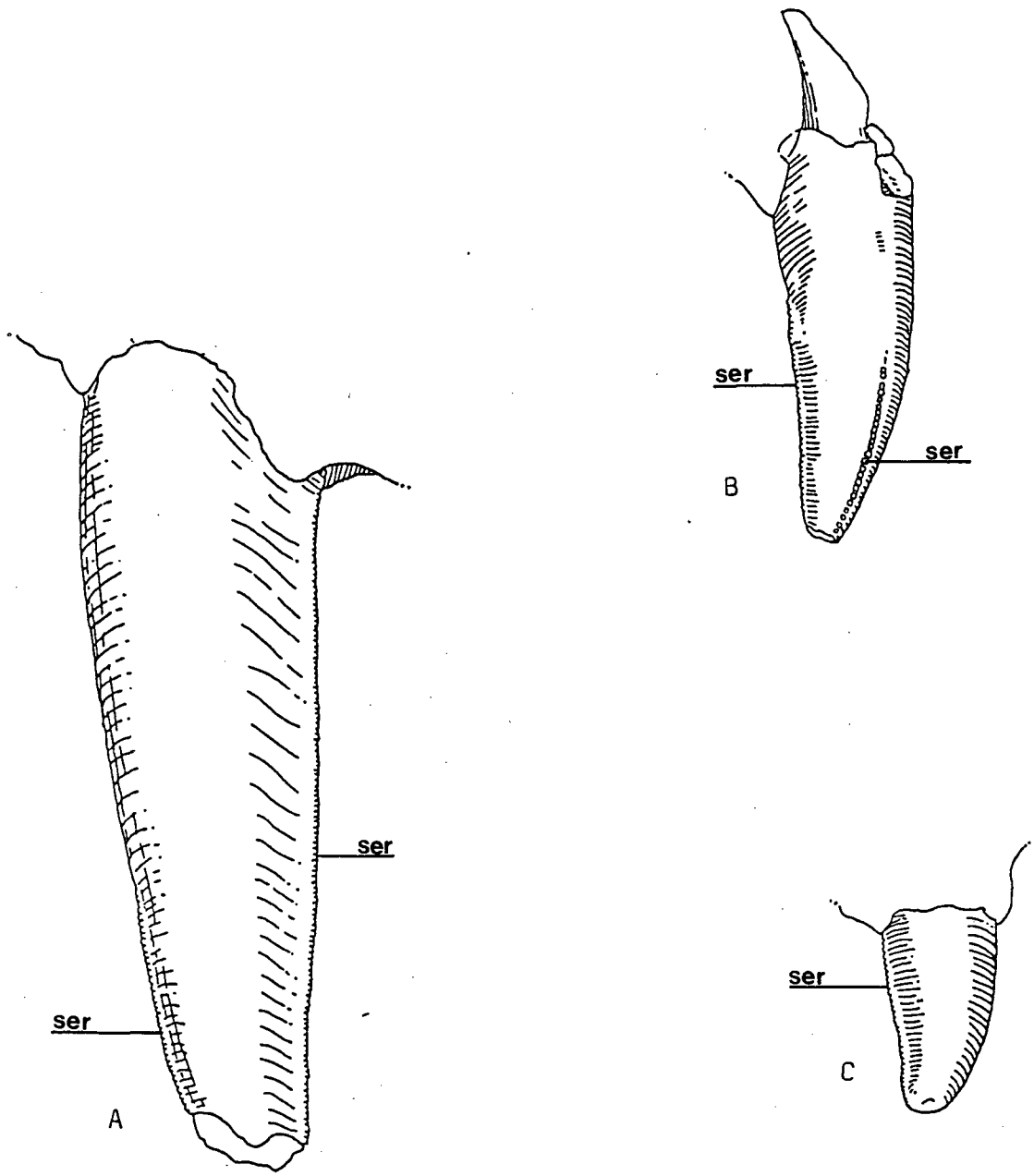

Fig. 33 Various types of early therocephalian teeth. A: canine, B: incisor C: postcanine. Scale 20mm.

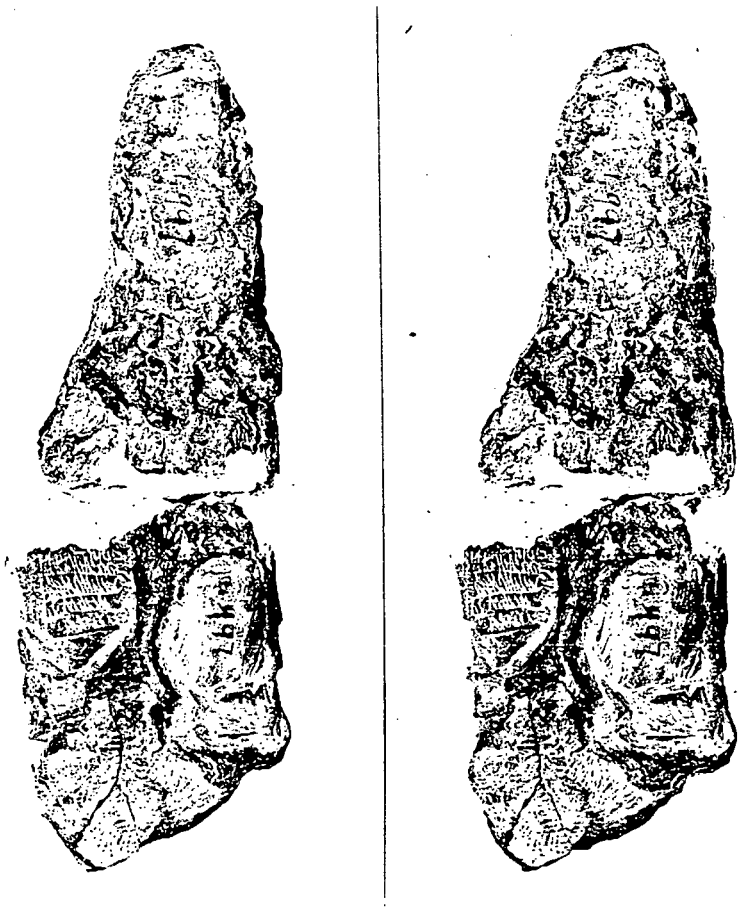

Fig. 34a Stereophotograph of the type skull of *Alopecideops gracilis* SAM 4997. Dorsal view. Scale 20mm.

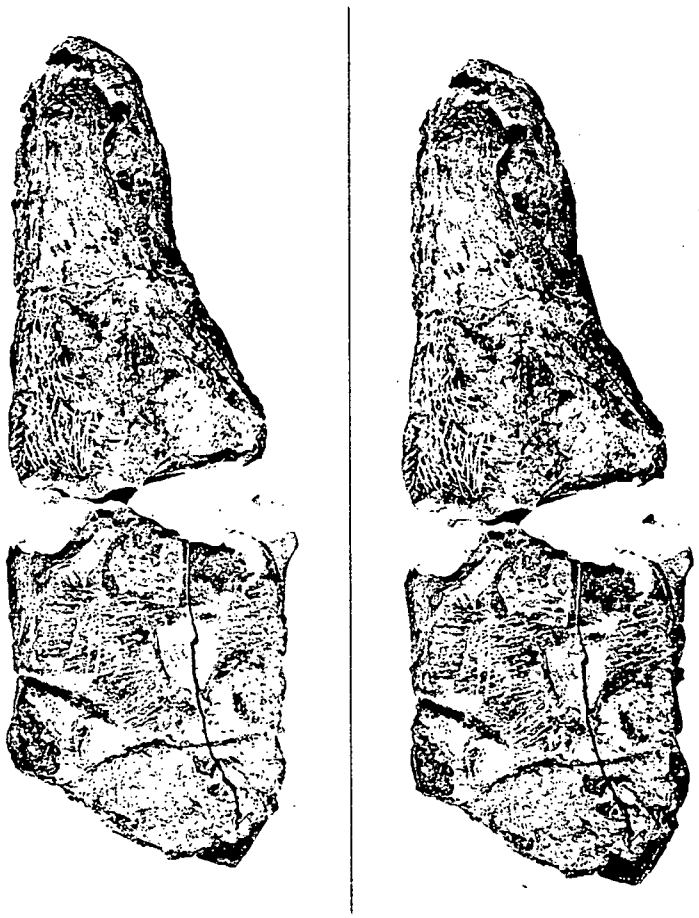

Fig. 34b Stereophotograph of the type skull of *Alopecideops gracilis* SAM 4997. Ventral view. Scale 20mm.

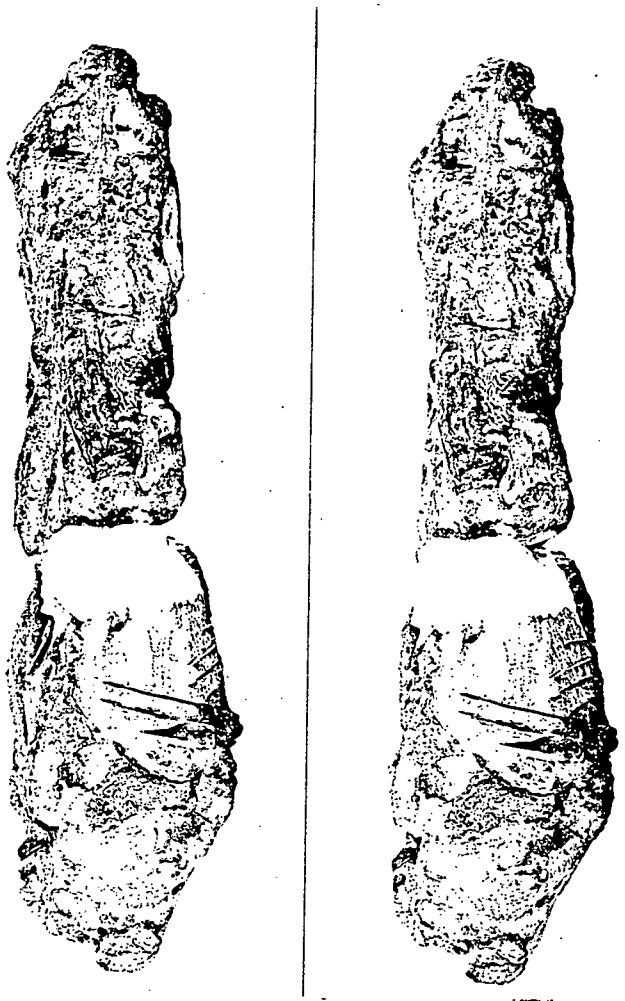

Fig. 34c Stereophotograph of the type skull of *Alopecideops gracilis* SAM 4997. Left lateral view. Scale 20mm.

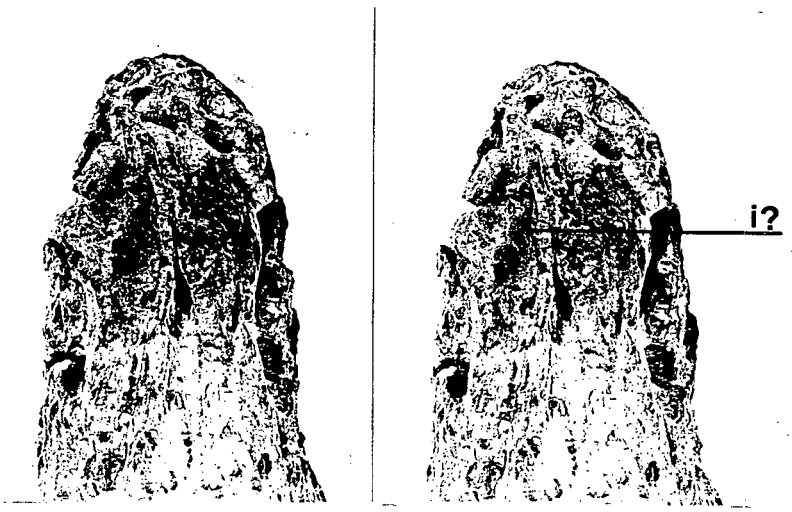

Fig. 34d Stereophotograph of the type skull of *Alopecideops gracilis* SAM 4997. Ventral close-up of snout and lower jaw. Scale 20mm.

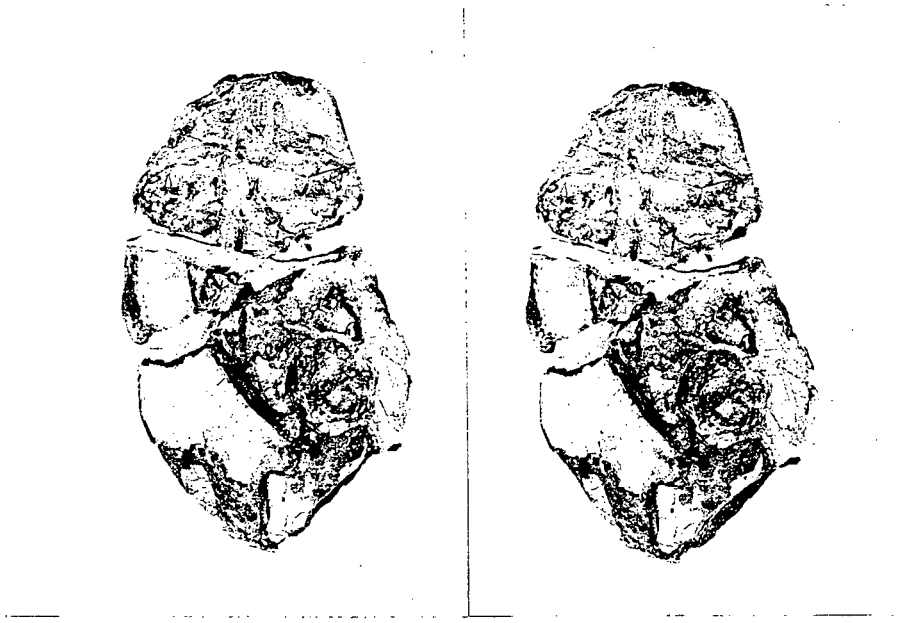

Fig. 35a Stereophotograph of the type skull of *Alopecodon priscus* SAM 920. Left lateral view. Scale 20mm.

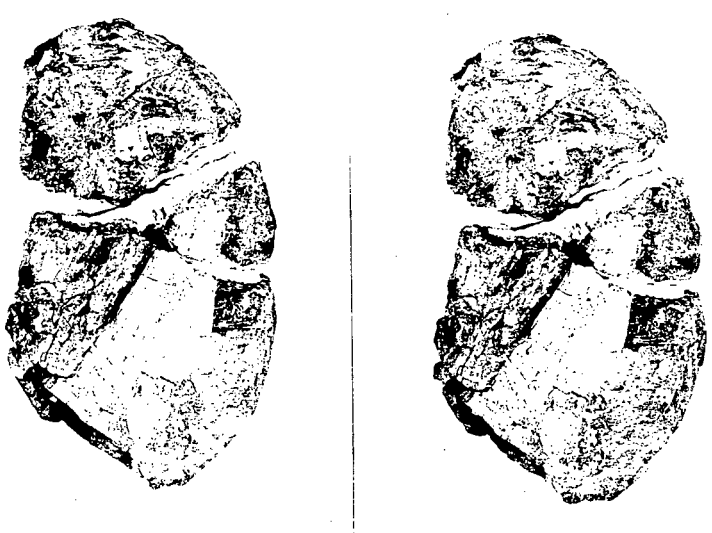

Fig. 35b Stereophotograph of the type skull of *Alopecodon priscus* SAM 920. Right lateral view. Scale 20mm.

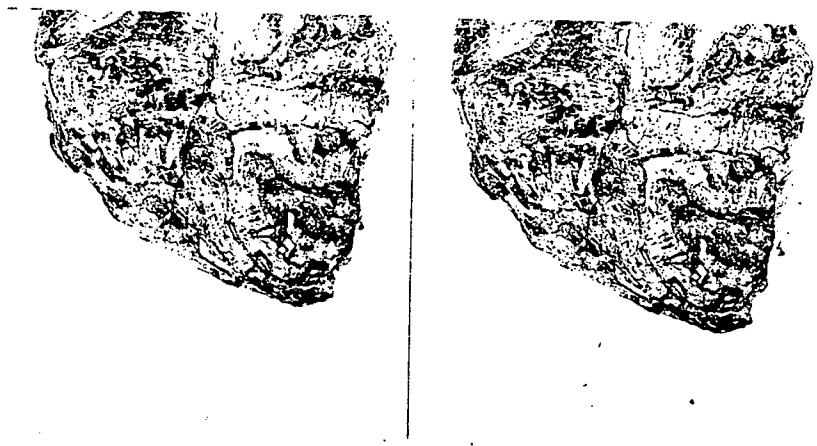

Fig. 35c Stereophotograph of incisor region of the type skull of *Alopecodon priscus* SAM 920. Left lateral view. Scale 20mm.

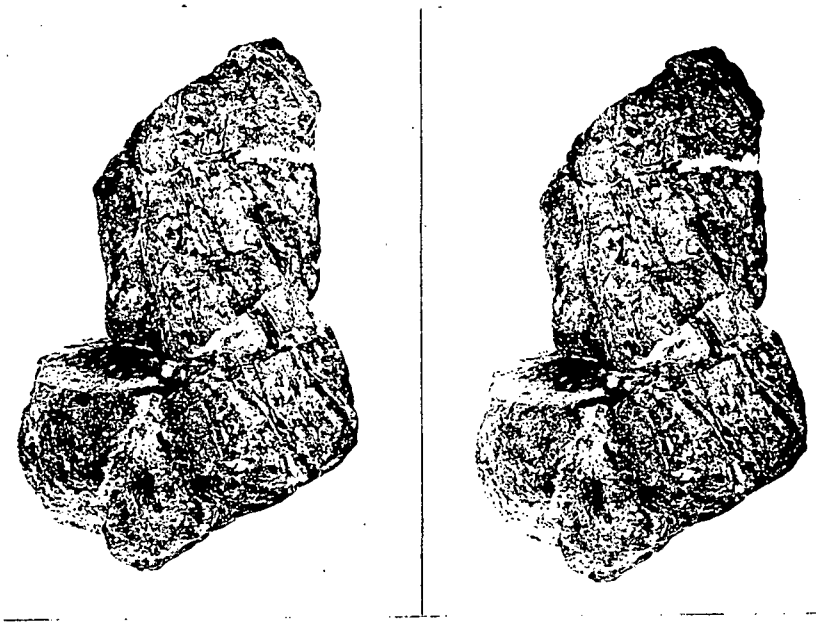

Fig. 36a Stereophotograph of the type skull of *Alopecodon rugosus* SAM 921. Left lateral view. Scale 20mm.

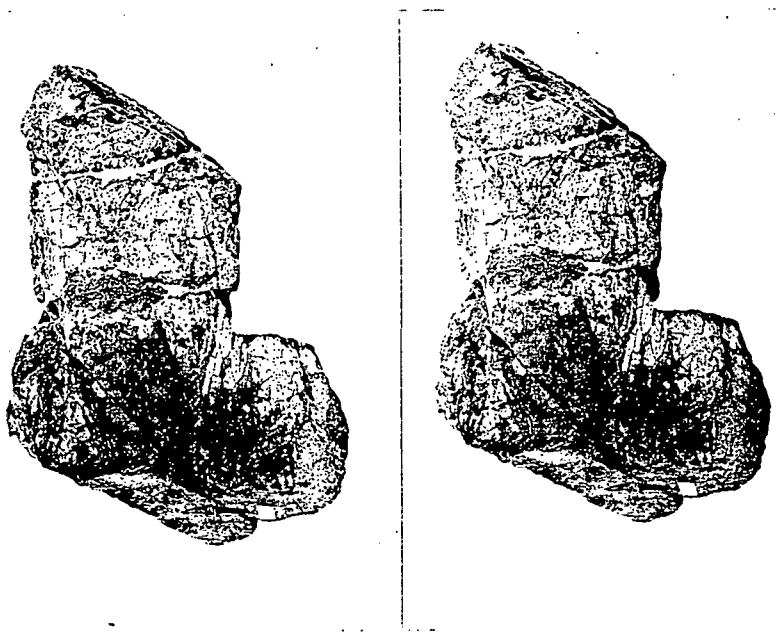

Fig. 36b Stereophotograph of the type skull of *Alopecodon rugosus* SAM 921. Right lateral view. Scale 20mm.

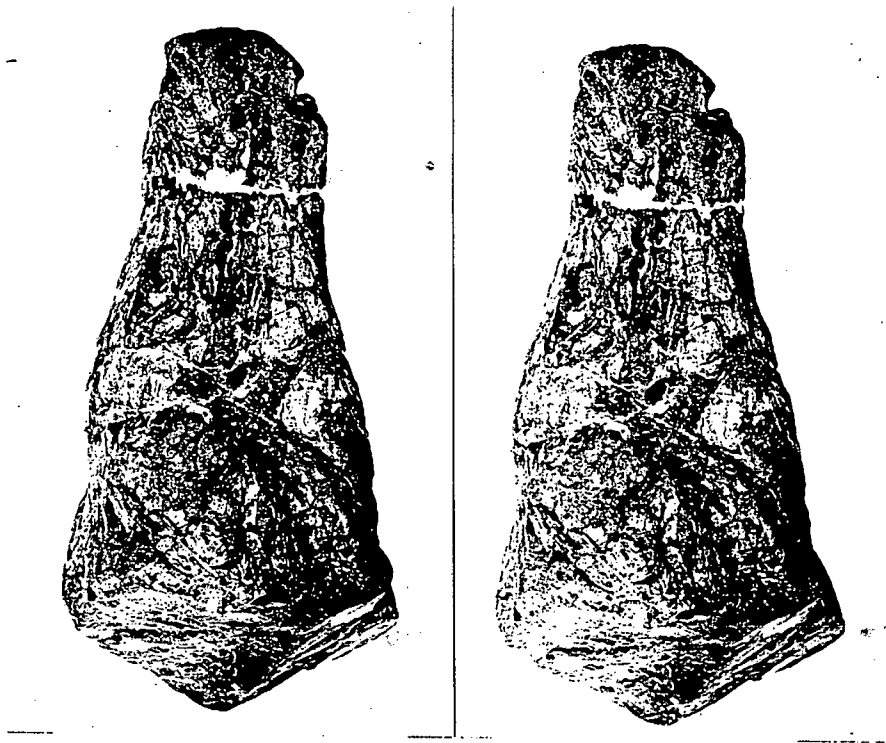

Fig. 36c Stereophotograph of the type skull of *Alopecodon rugosus* SAM 921. Dorsal view. Scale 20mm.

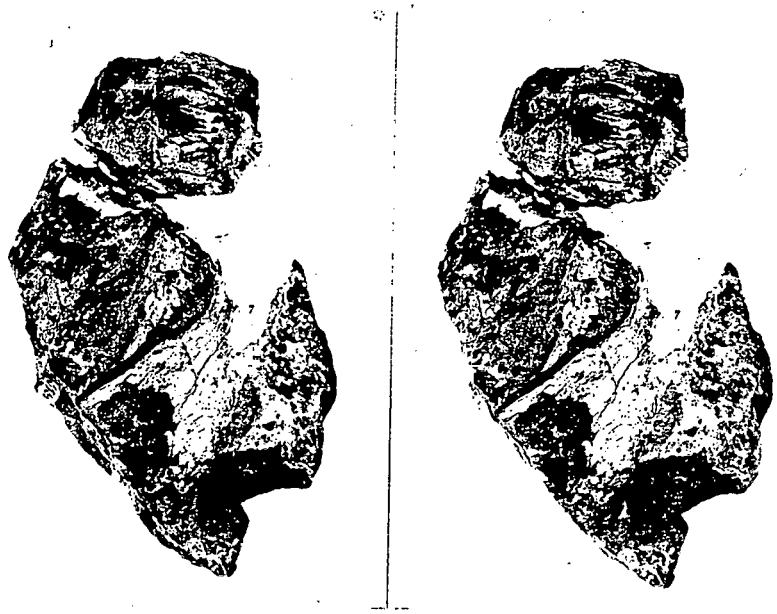

Fig. 37 Stereophotograph of AMNH 5569 ***Alopecodon priscus***. Right lateral view. Scale 20mm.

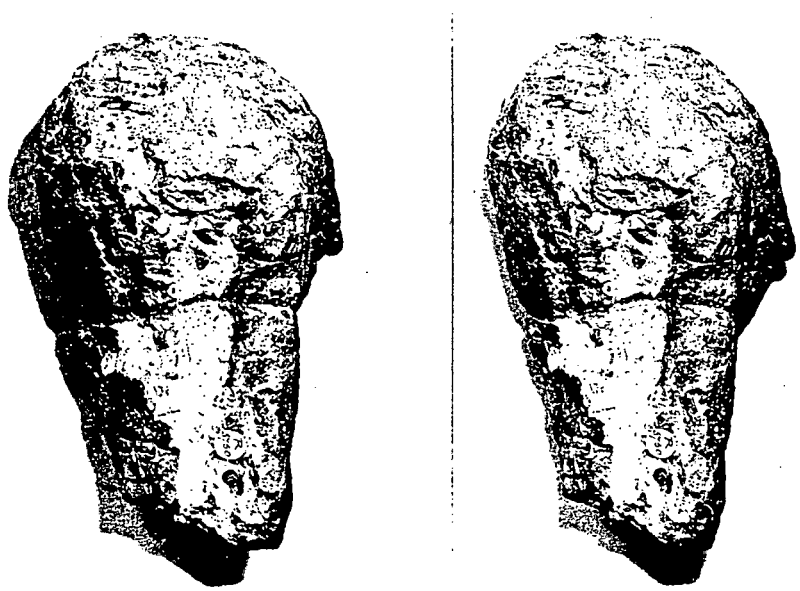

Fig. 38 Stereophotograph of the type of ***Alopecodon minor*** BMNH R5750. Right lateral view. Scale 20mm.

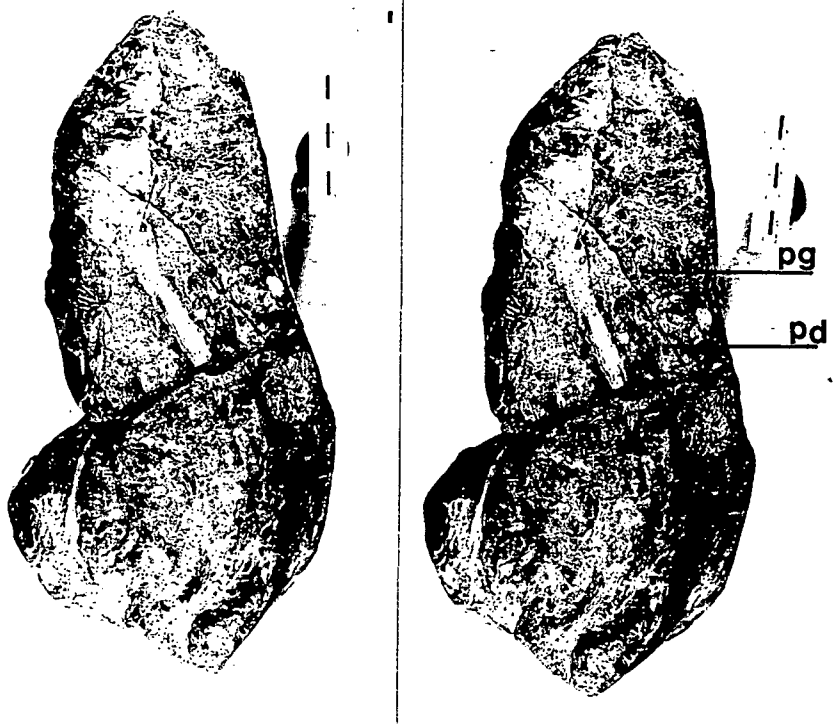

Fig. 39a Stereophotograph of the type of *Alopecognathus angusticeps* AMNH 5559. Left lateral view. Scale 20mm.

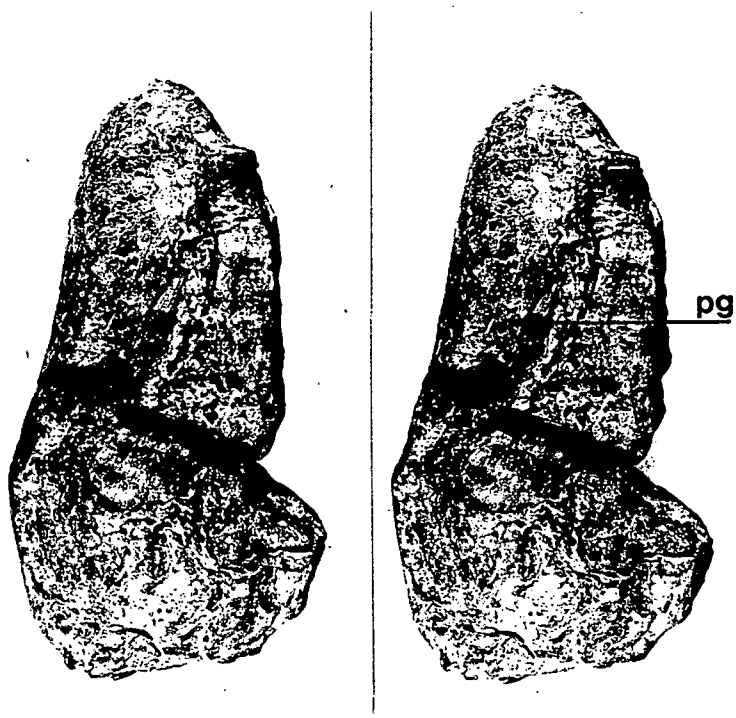

Fig. 39b Stereophotograph of the type of *Alopecognathus angusticeps* AMNH 5559. Right lateral view. Scale 20mm.

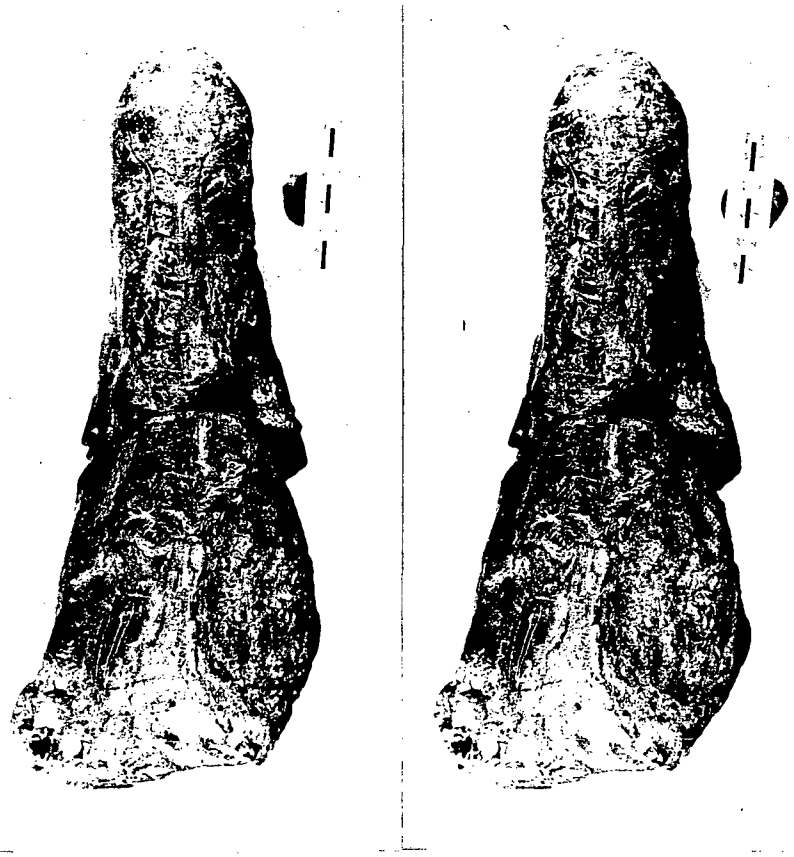

Fig. 39c Stereophotograph of the type of *Alopecognathus angusticeps* AMNH 5559. Dorsal view. Scale 20mm.

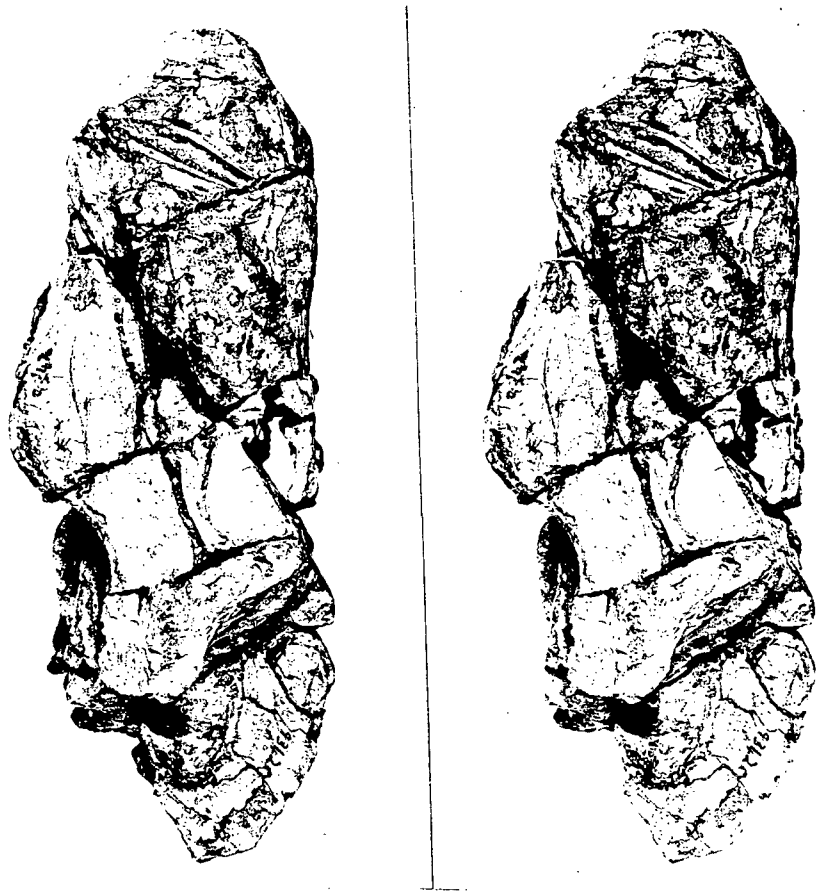

Fig. 40a Stereophotograph of the type skull of *Alopecognathus angustioriceps* SAM 9342. Left lateral view. Scale 20mm.

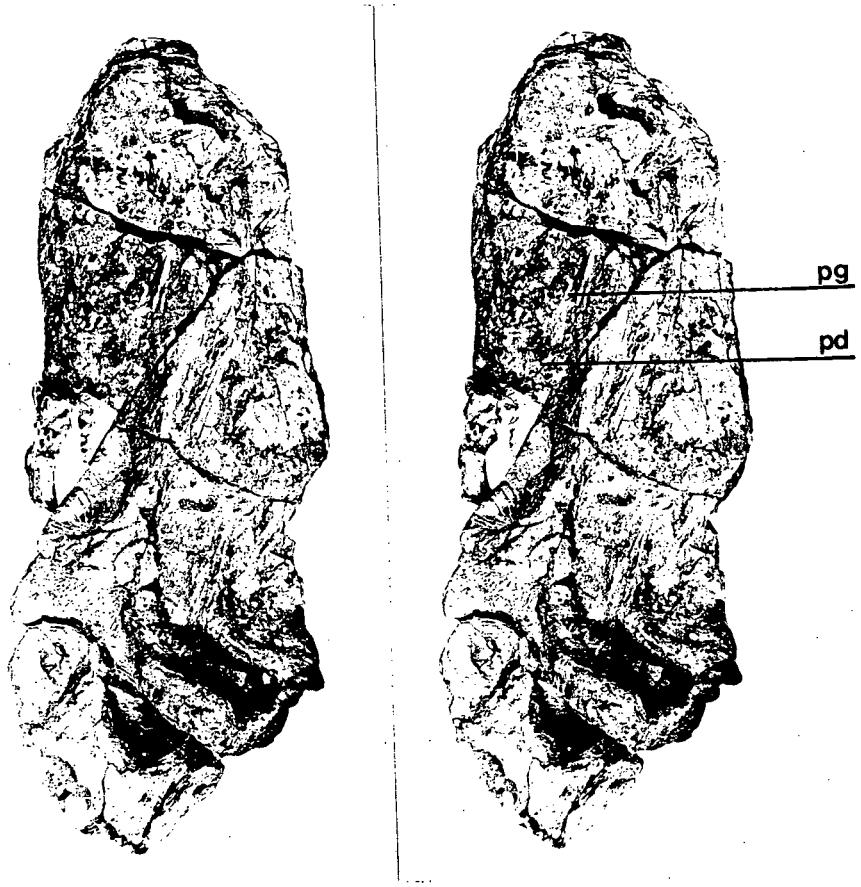

Fig. 40b Stereophotograph of the type skull of ***Alopecognathus angustioriceps*** SAM 9342. Right lateral view. Scale 20mm.

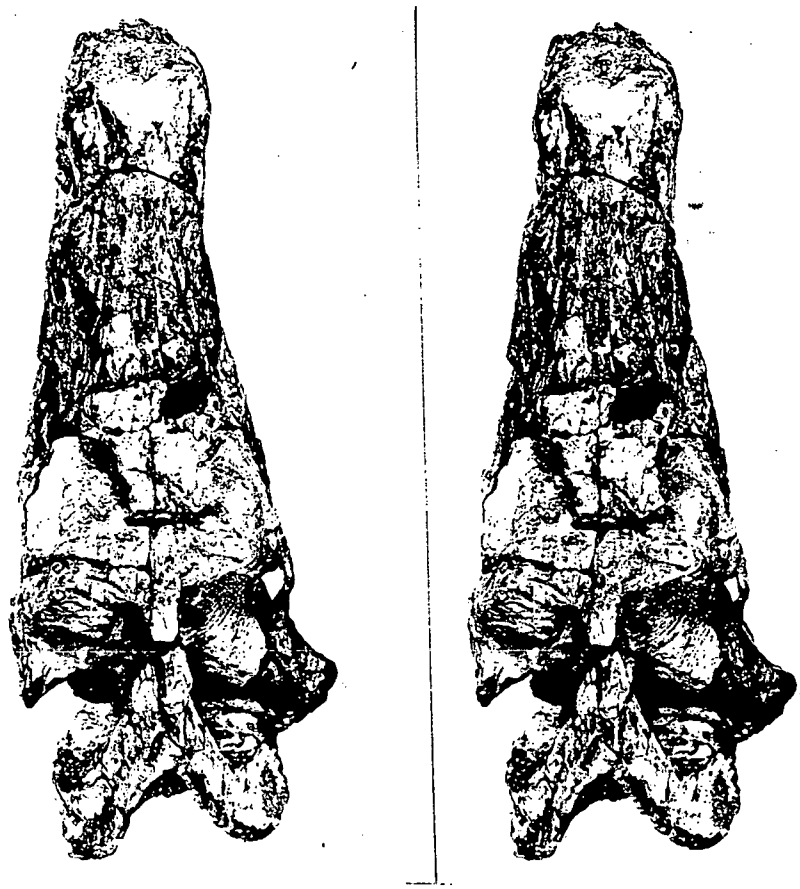

Fig. 40c Stereophotograph of the type skull of *Alopecognathus angustioriceps* SAM 9342. Dorsal view. Scale 20mm.

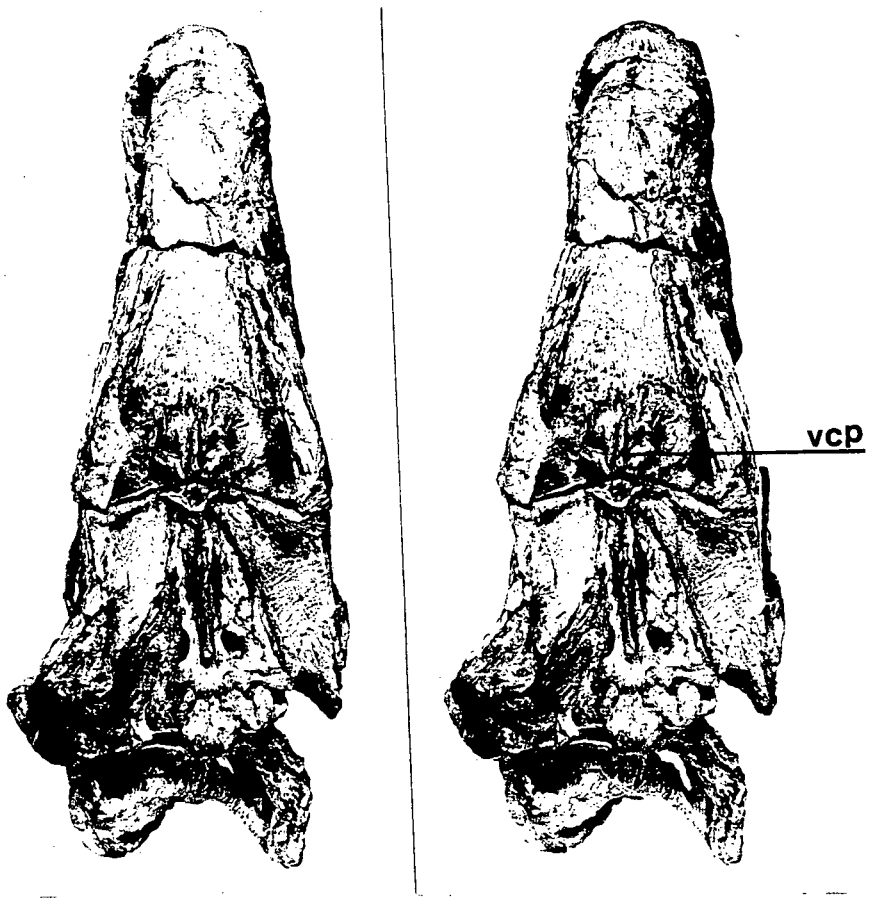

Fig. 40d Stereophotograph of the type skull of *Alopecognathus angustioriceps* SAM 9342. Ventral view. Scale 20mm.

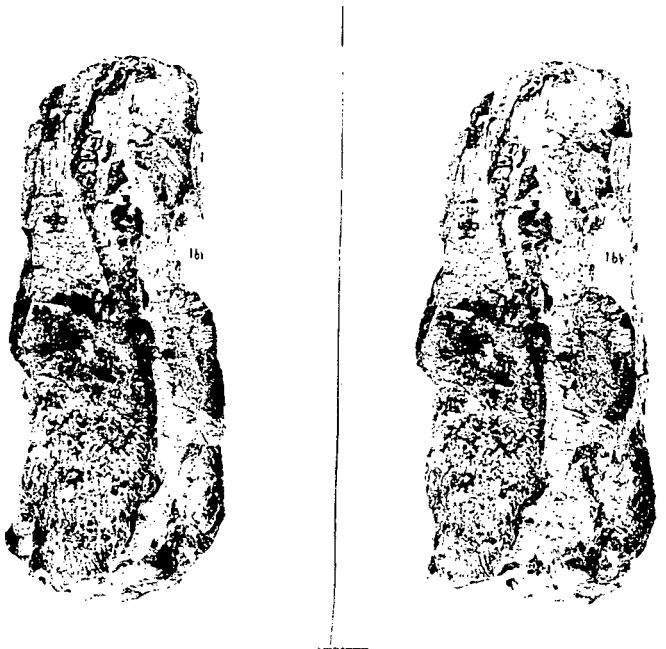

Fig. 41a Stereophotograph of the type skull of ***Alopecognathus megalops*** TM 1491. Left lateral view. Scale 20mm.

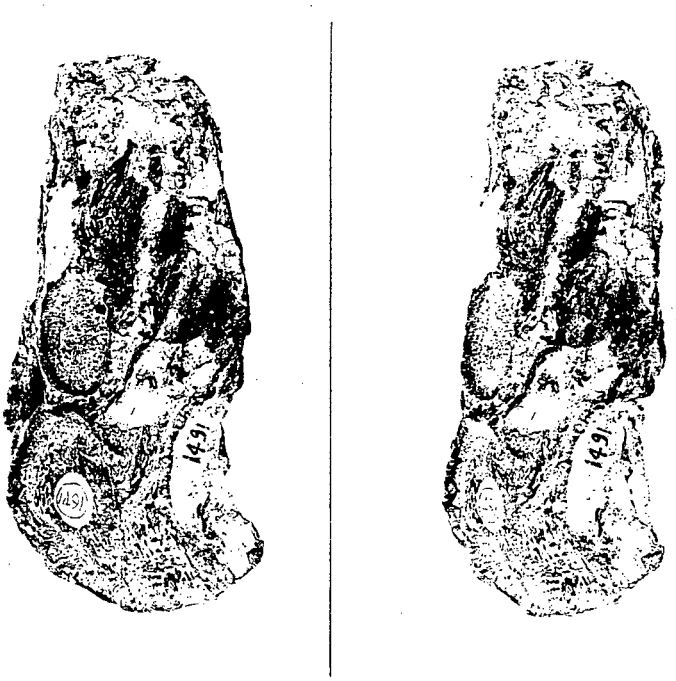

Fig. 41b Stereophotograph of the type skull of ***Alopecognathus megalops*** TM 1491. Right lateral view. Scale 20mm.

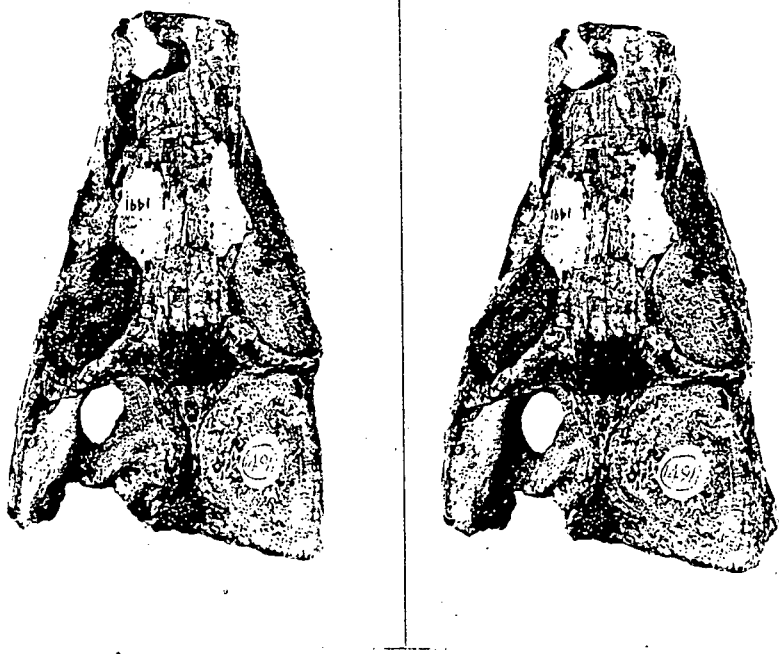

Fig. 41c Stereophotograph of the type skull of *Alopecognathus megalops* TM 1491. Dorsal view. Scale 20mm.

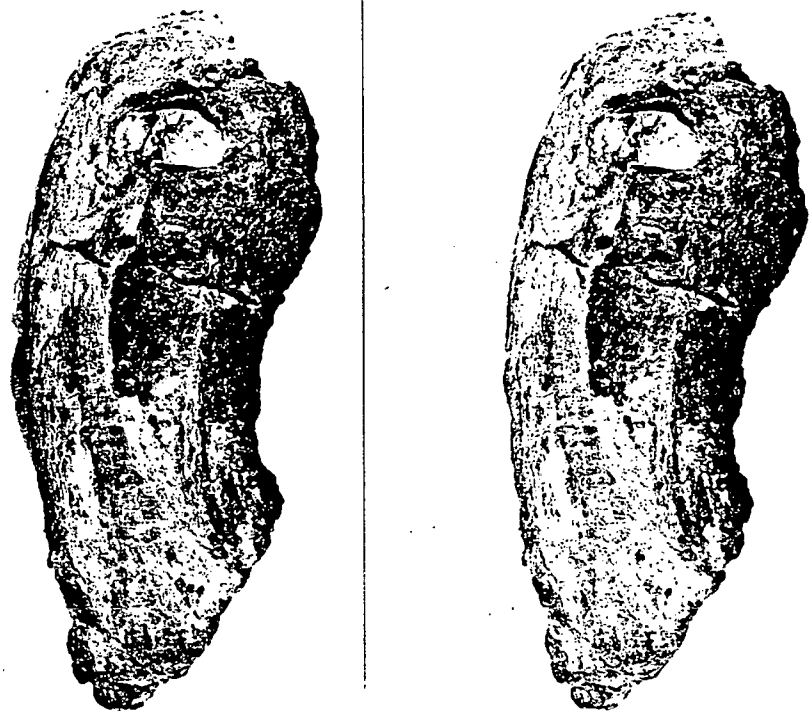

Fig. 42a Stereophotograph of the type of ***Alopecorhinus parvidens*** AMNH 5503. Left lateral view. Scale 20mm.

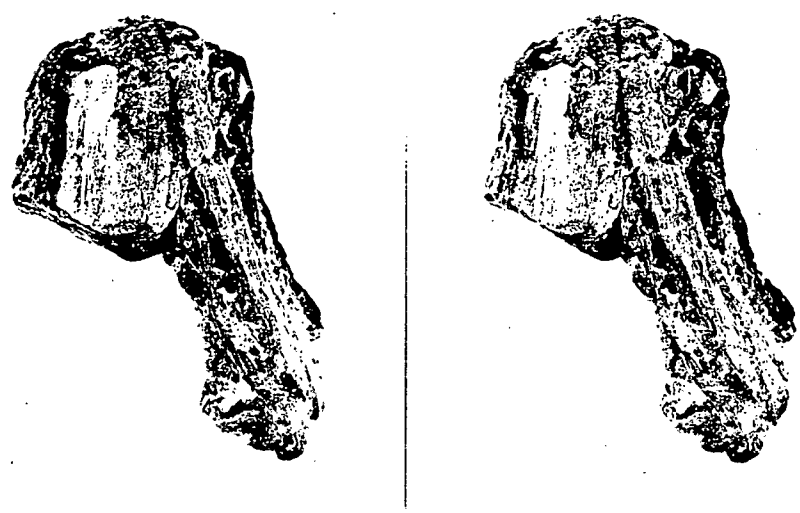

Fig. 42b Stereophotograph of the type of ***Alopecorhinus parvidens*** AMNH 5503. Ventral view. Scale 20mm.

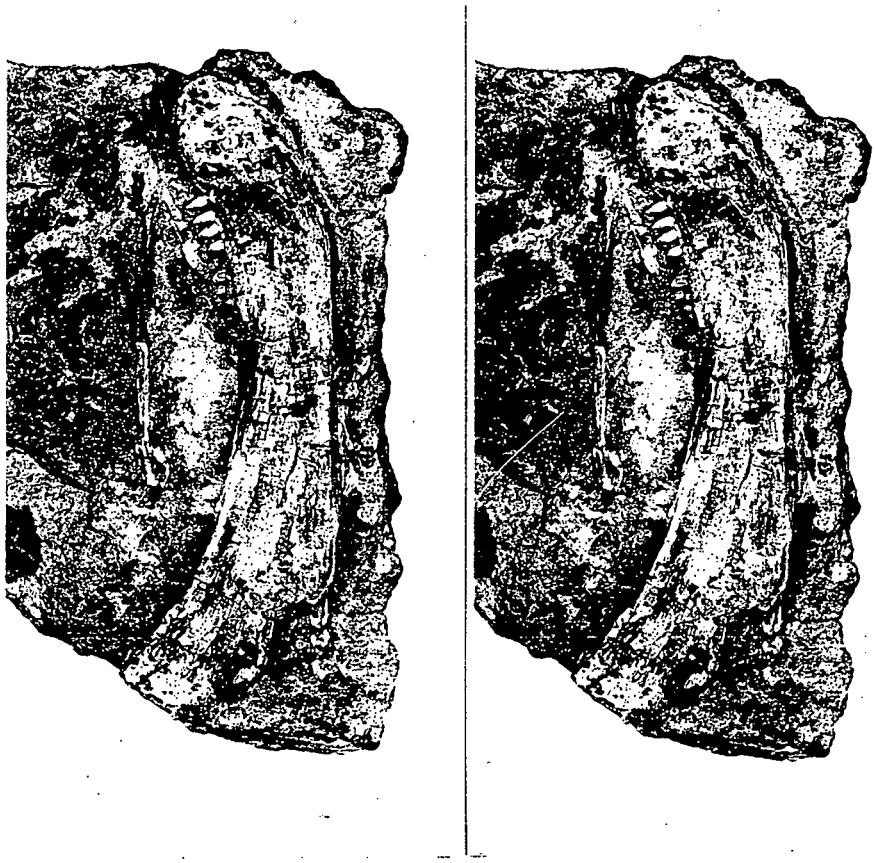

Fig. 43 Stereophotograph of the right lower jaw ramus of the type of *Arnognathus parvidens* SAM 1069. Lateral view. Scale 20mm.

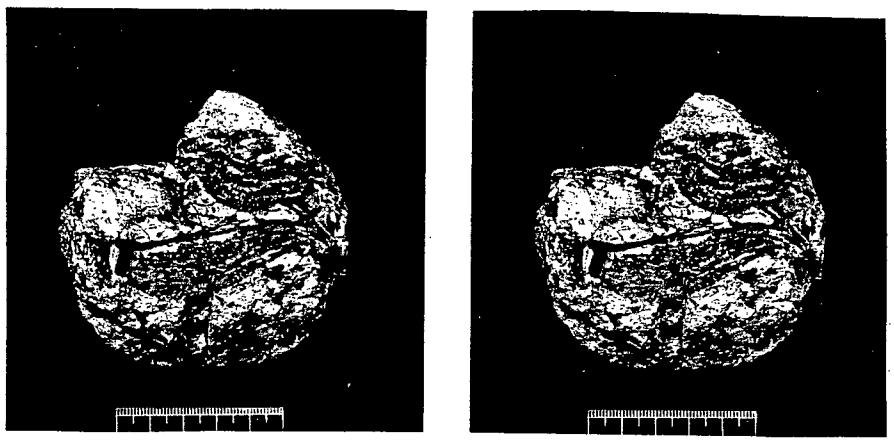

Fig. 44 Stereophotograph of the type skull of *Cerdodon tenuidens* BMNH 49420. Left lateral view. Scale 50mm.

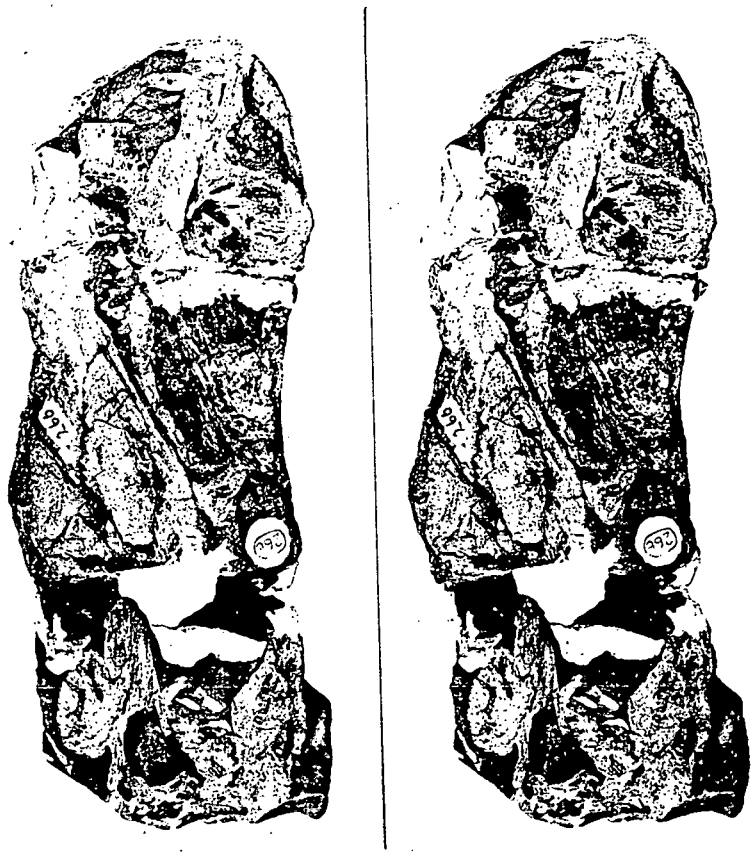

Fig. 45a Stereophotograph of the type skull of *Cynariognathus galloweyi* TM 266. Left lateral view. Scale 20mm.

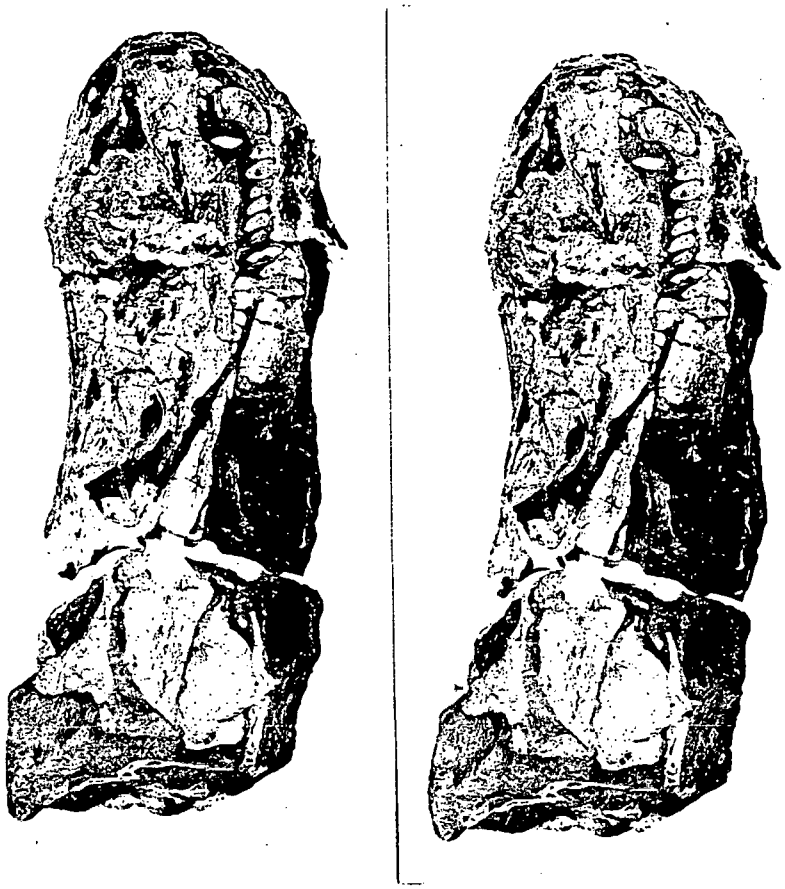

Fig. 45b Stereophotograph of the type skull of *Cynariognathus gallowayi* TM 266. Right lateral view. Scale 20mm.

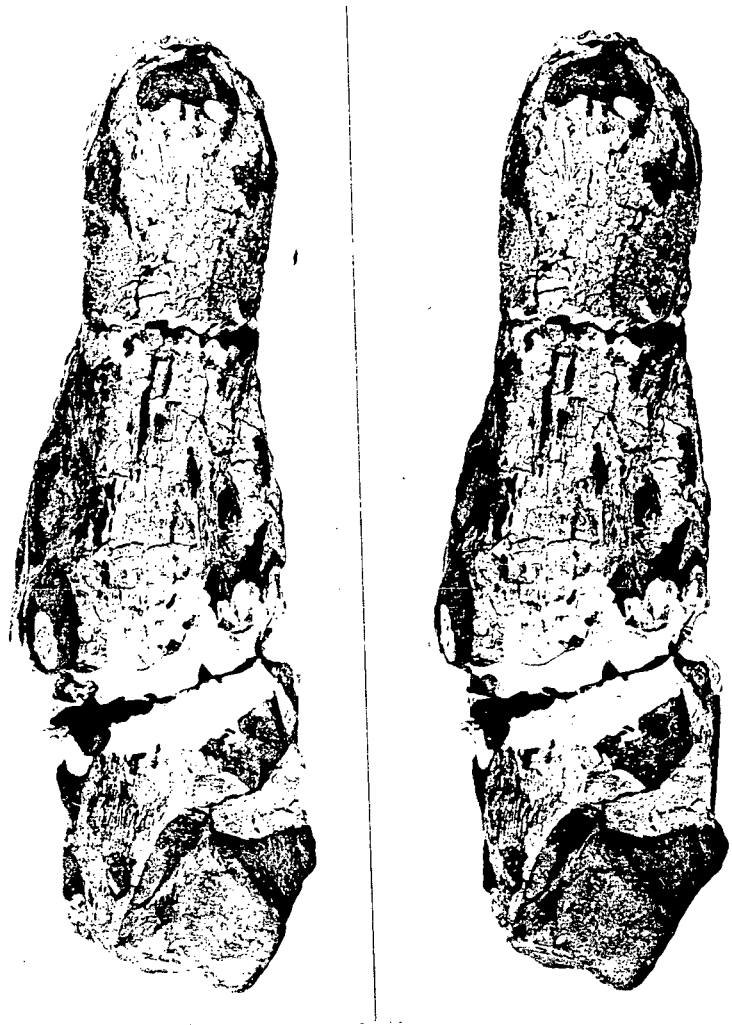

Fig. 45c Stereophotograph of the type skull of *Cynariognathus gallowayi* TM 266. Dorsal view. Scale 20mm.

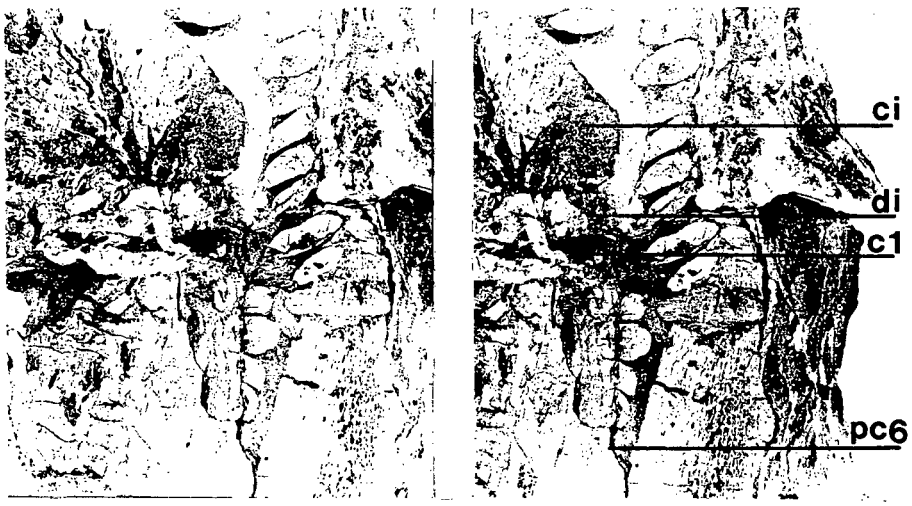

Fig 45d Stereophotograph of the type skull of *Cynariognathus gallowayi* TM 266. Close-up of right postcanine series. Scale 20mm.

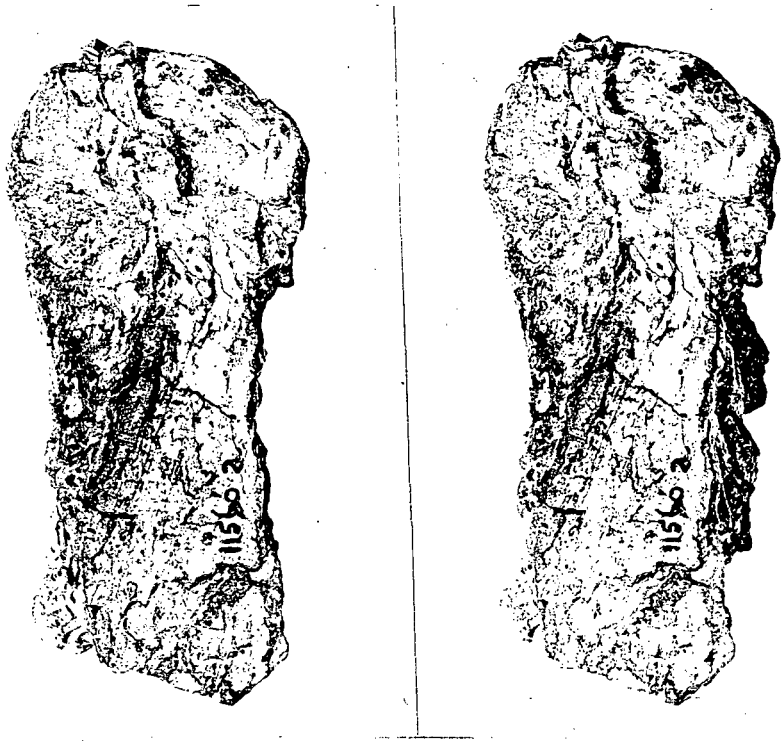

Fig. 46a Stereophotograph of the type skull of ***Cynariognathus paucioridens*** SAM 11560a. Right lateral view. Scale 20mm.

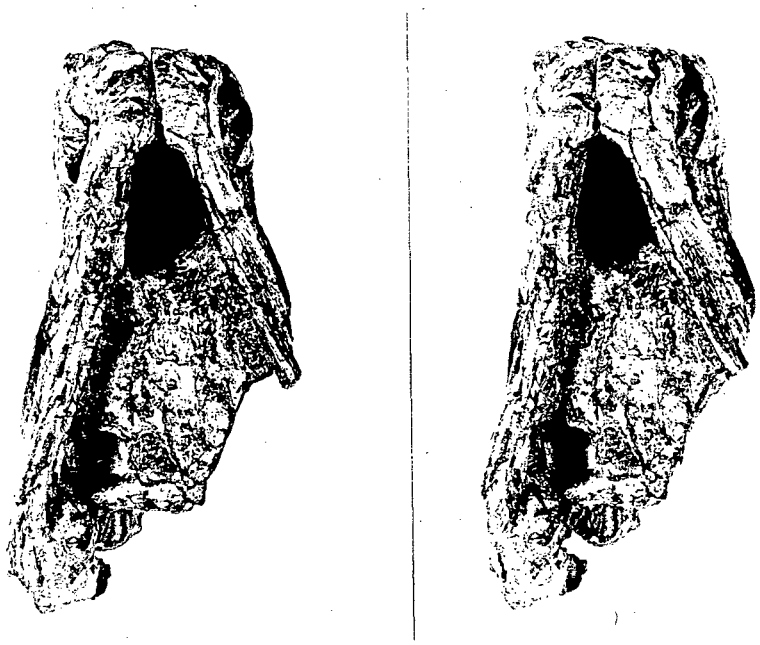

Fig. 46b Stereophotograph of the type skull of ***Cynariognathus paucioridens*** SAM 11560a. Ventral view. Scale 20mm.

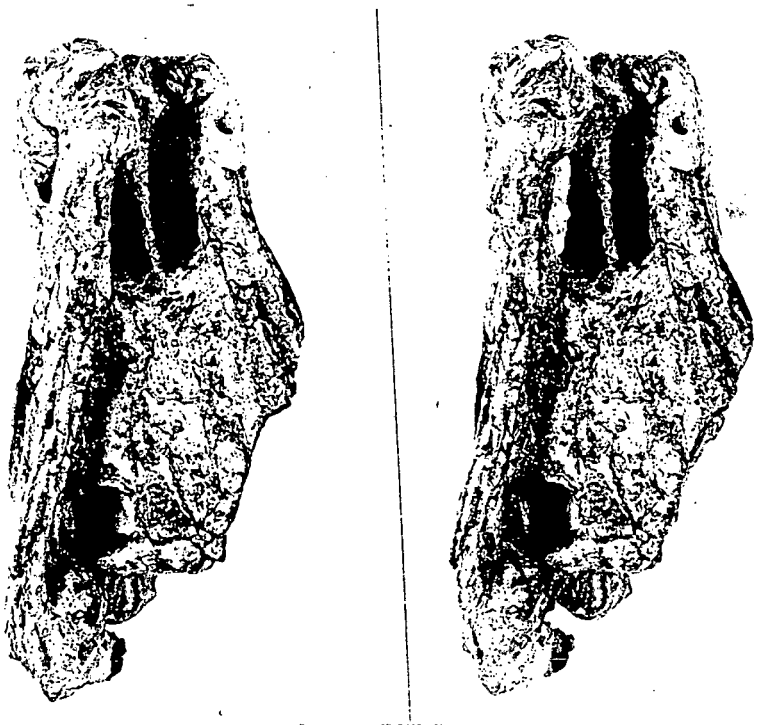

Fig. 46c Stereophotograph of the type skull of *Cynariognathus pauciroidens* SAM 11560a. Ventral view with left jaw ramus removed. Scale 20mm.

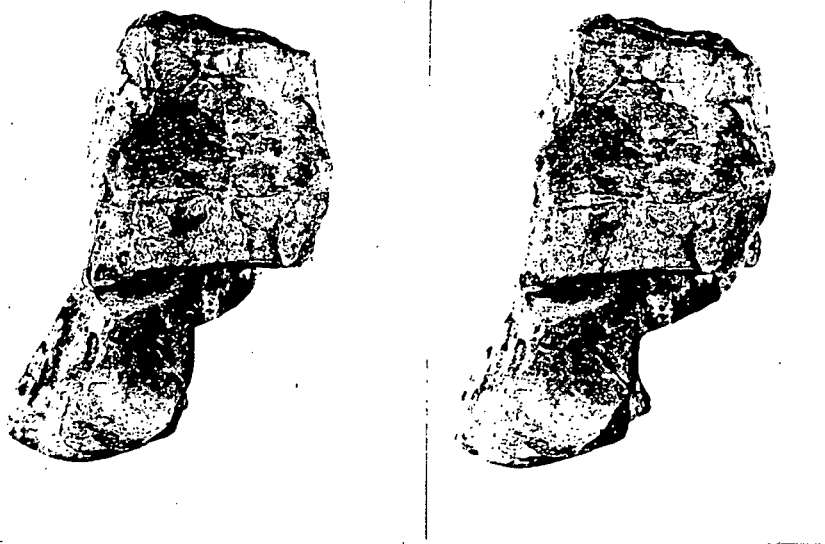

Fig. 47a Stereophotograph of the type of ***Cynariognathus platyrhinus*** AMNH 5502. Dorsal view. Scale 20mm.

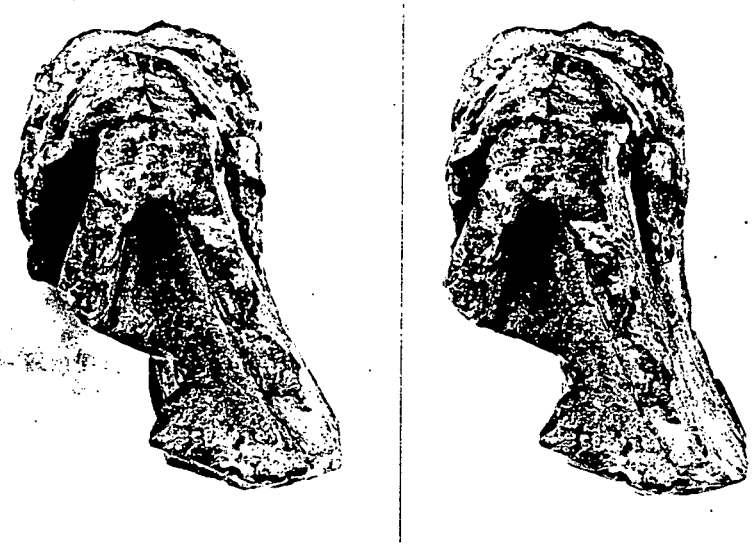

Fig. 47b Stereophotograph of the type of ***Cynariognathus platyrhinus*** AMNH 5502. Ventral view. Scale 20mm.

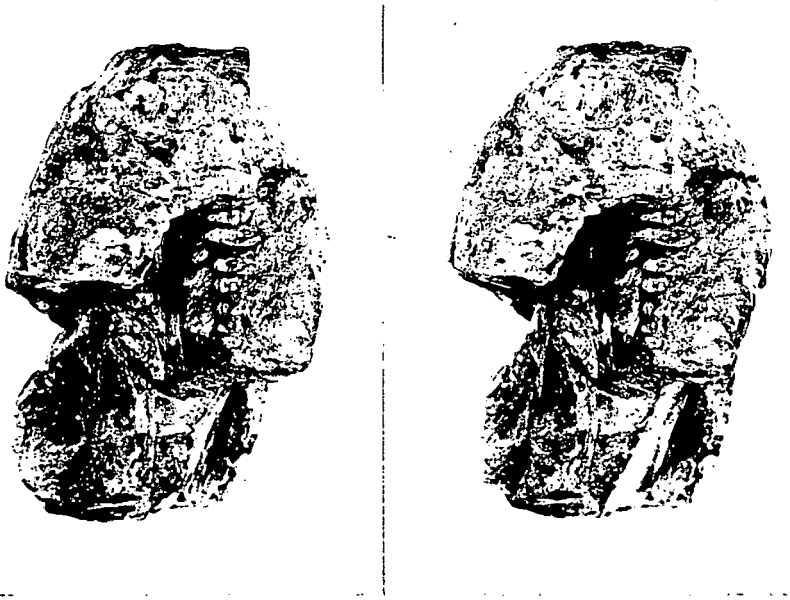

Fig. 47c Stereophotograph of the type of *Cynariognathus platyrhinus* AMNH 5502. Right lateral view. Scale 20mm.

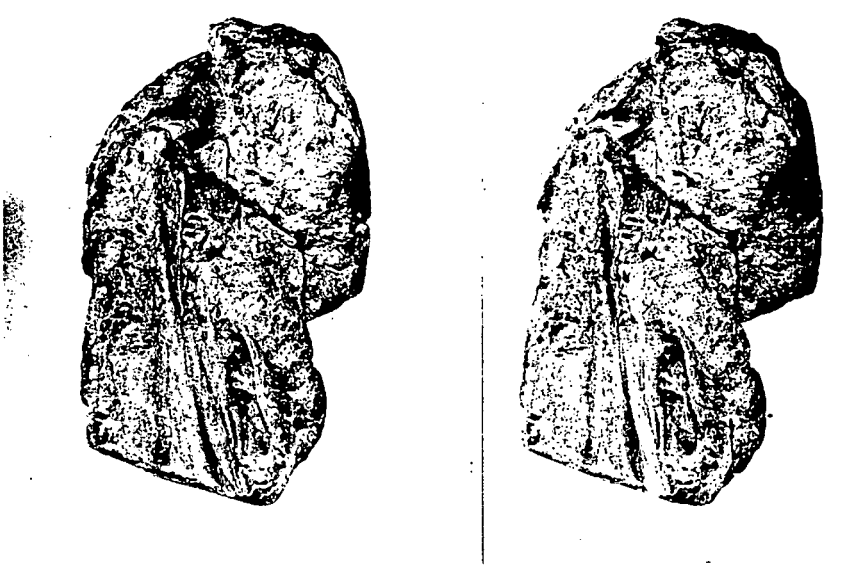

Fig. 47d Stereophotograph of the type of *Cynariognathus platyrhinus* AMNH 5502. Left lateral view. Scale 20mm.

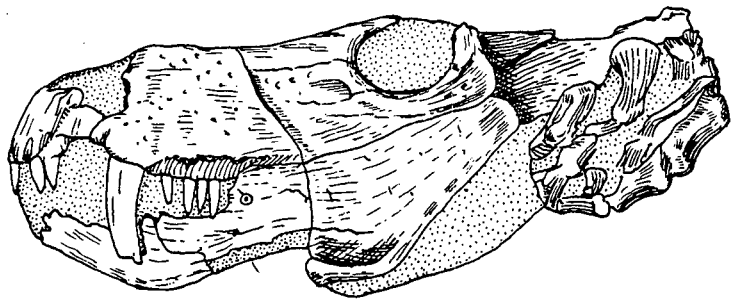

Fig. 48a Left lateral view of the type skull of ***Cynariognathus seeleyi*** UM 1934 VIII 30. After Broili & Schröder (1936a). Scale 20mm.

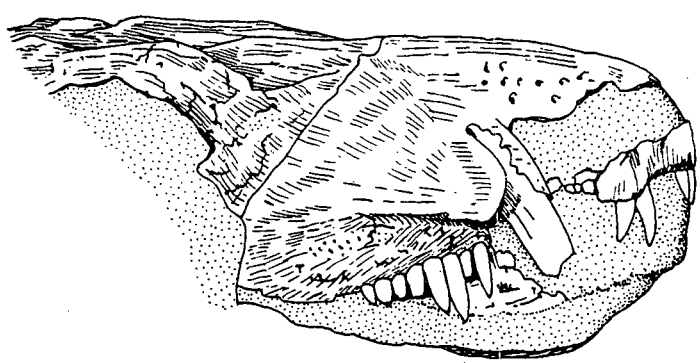

Fig. 48b Right lateral view of the type skull of ***Cynariognathus seeleyi*** UM 1934 VIII 30. After Broili & Schröder (1936a). Scale 20mm.

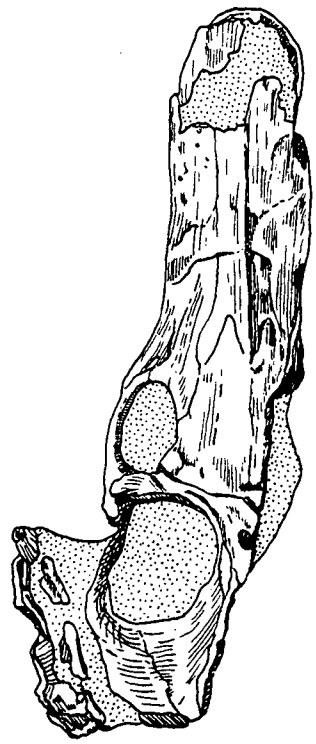

Fig. 48c Dorsal view of the type skull of *Cynariognathus seeleyi* UM 1934 VIII 30. After Broili & Schröder (1936a). Scale 20mm.

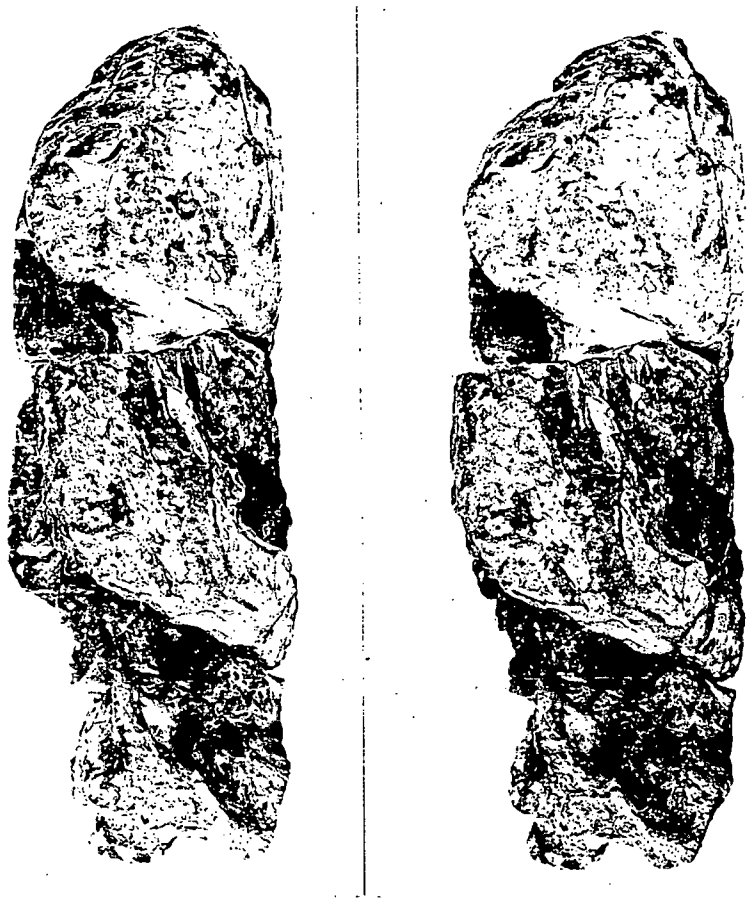

Fig. 49a Stereophotograph of the type skull of ***Glanosuchus macrops*** SAM 637. Left lateral view. Scale 20mm.

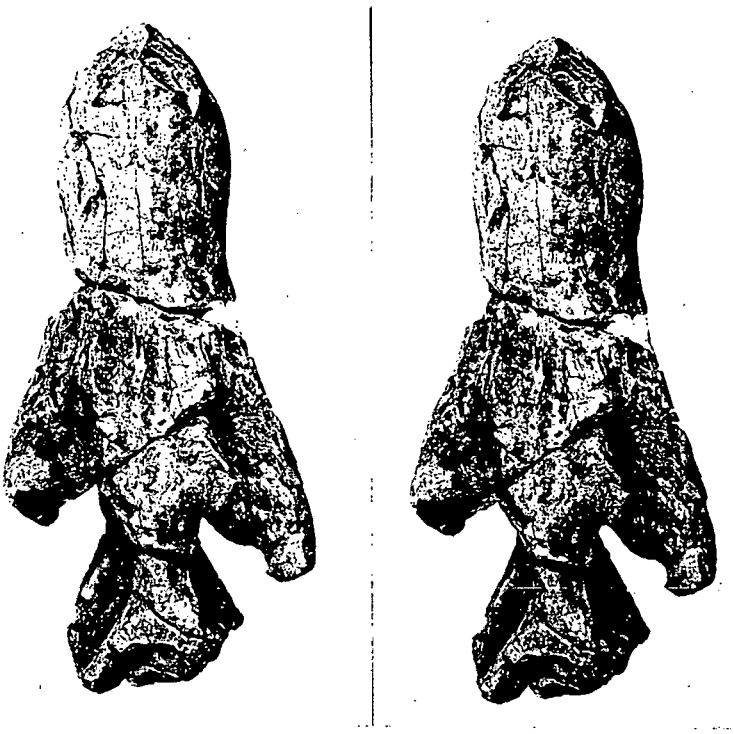

Fig. 49b Stereophotograph of the type skull of *Glanosuchus macrops* SAM 637. Dorsal view. Scale 20mm.

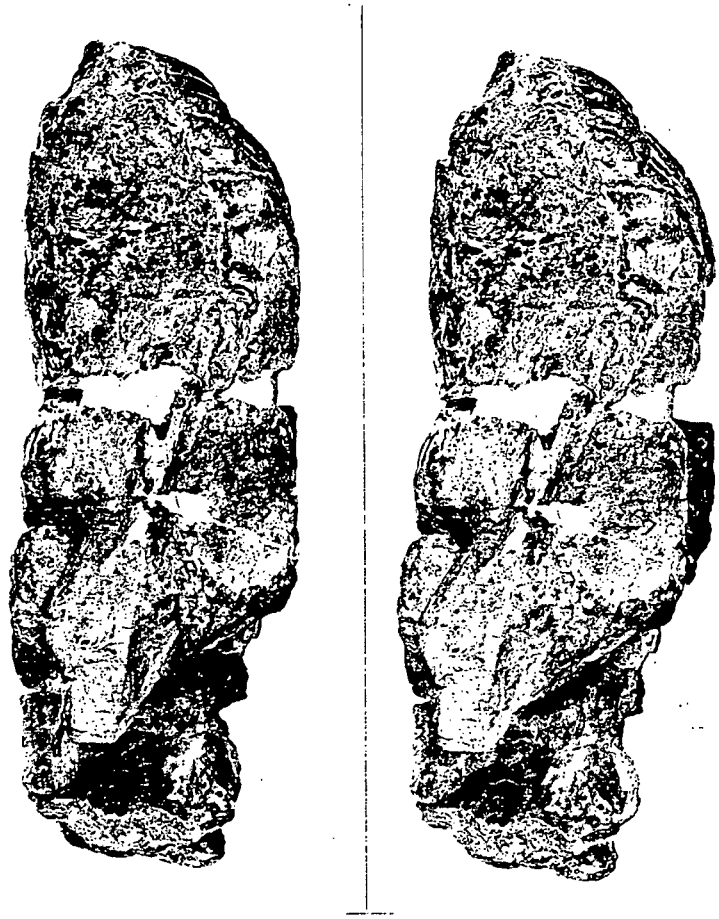

Fig. 49c Stereophotograph of the type skull of *Glanosuchus macrops* SAM 637. Right lateral view. Scale 20mm.

Fig. 49d Stereophotograph of the type skull of *Glanosuchus macrops* SAM 637. Ventral view of interpterygoid region. Scale 20mm.

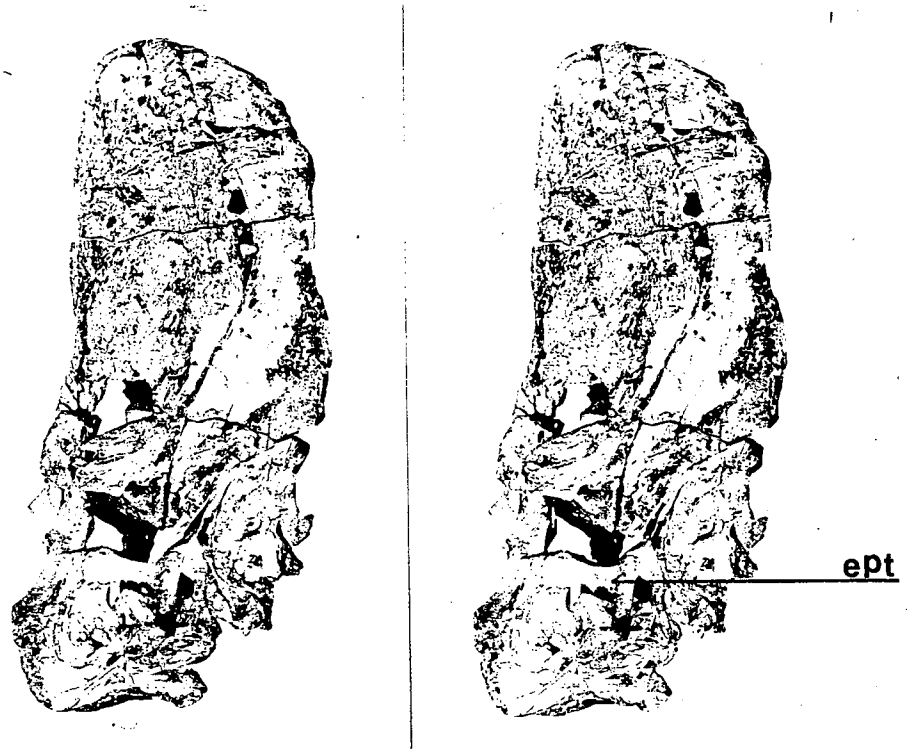

Fig. 50a Stereophotograph of *Glanosuchus macrops* GS M796. Right lateral view of skull and lower jaw. Scale 20mm.

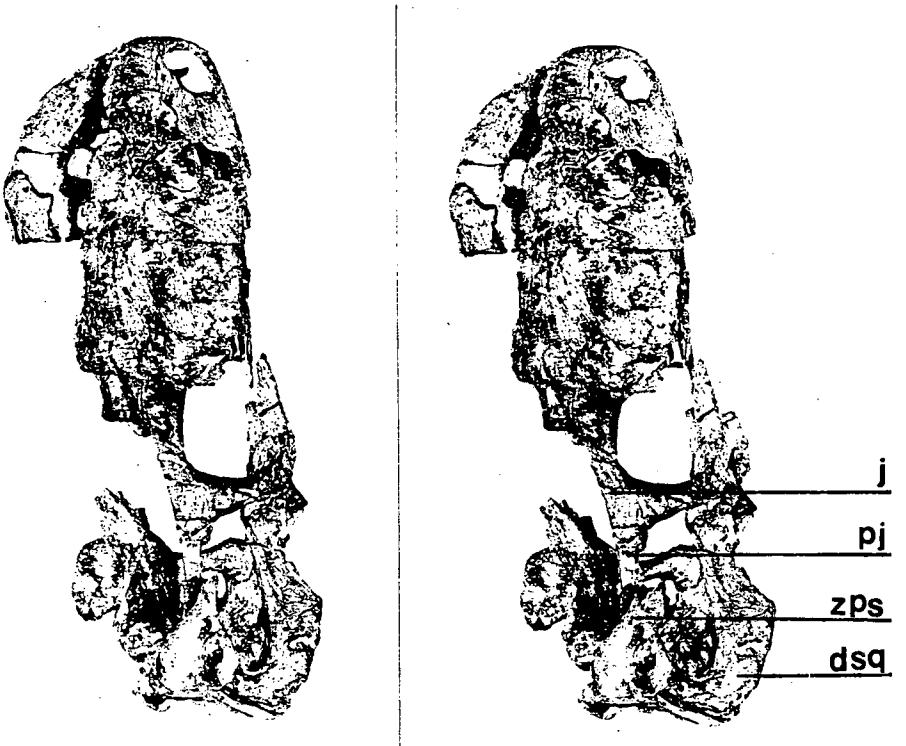

Fig. 50b Stereophotograph of *Glanosuchus macrops* GS M796. Left lateral view of skull. Scale 20mm.

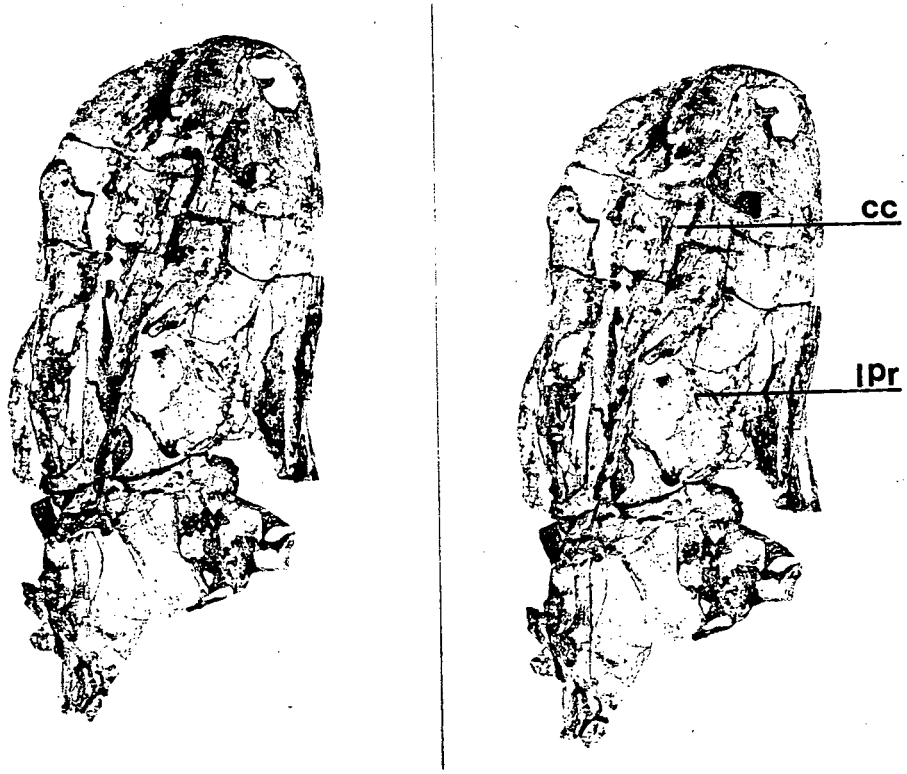

Fig. 50c Stereophotograph of *Glanosuchus macrops* GS M796. Medial view of right half of skull and lower jaw. Scale 20mm.

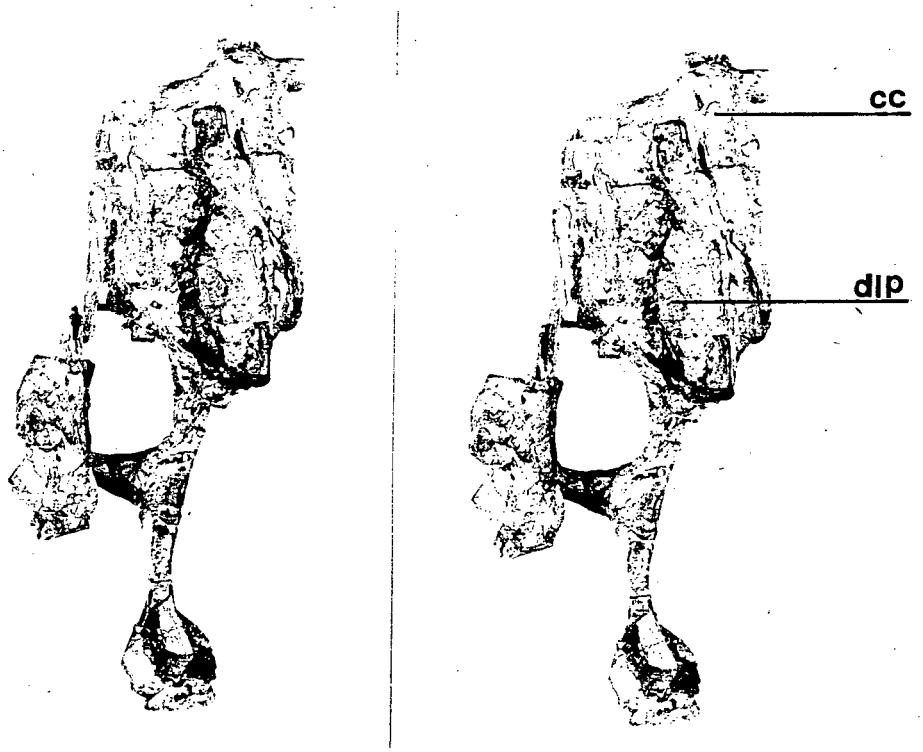

Fig. 50d Stereophotograph of *Glanosuchus macrops* GS M796. Medial view of left half of skull. Scale 20mm.

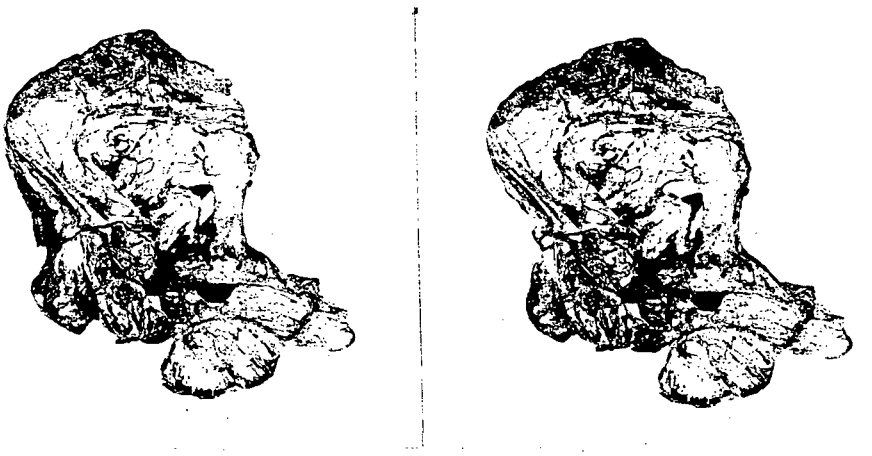

Fig. 50e Stereophotograph of *Glanosuchus macrops* GS M796. Right lateral view of braincase. Scale 20mm.

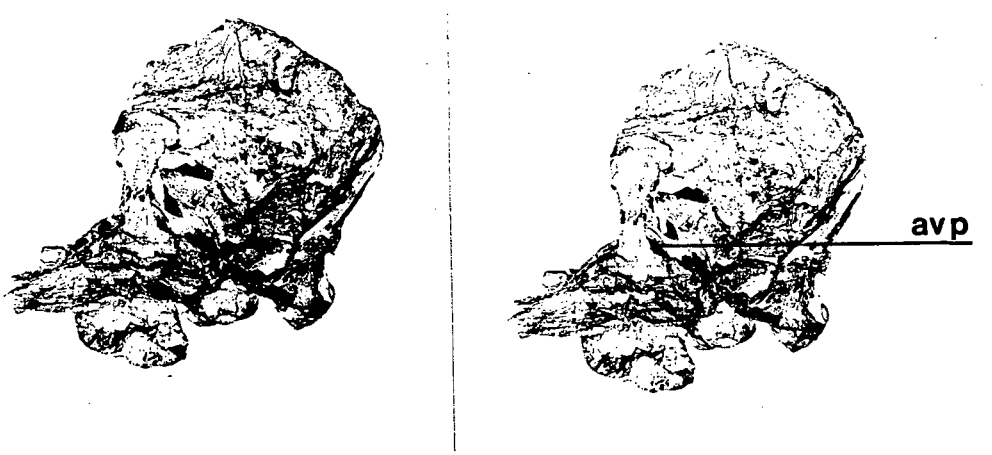

Fig. 50f Stereophotograph of *Glanosuchus macrops* GS M796. Left lateral view of braincase. Scale 20mm.

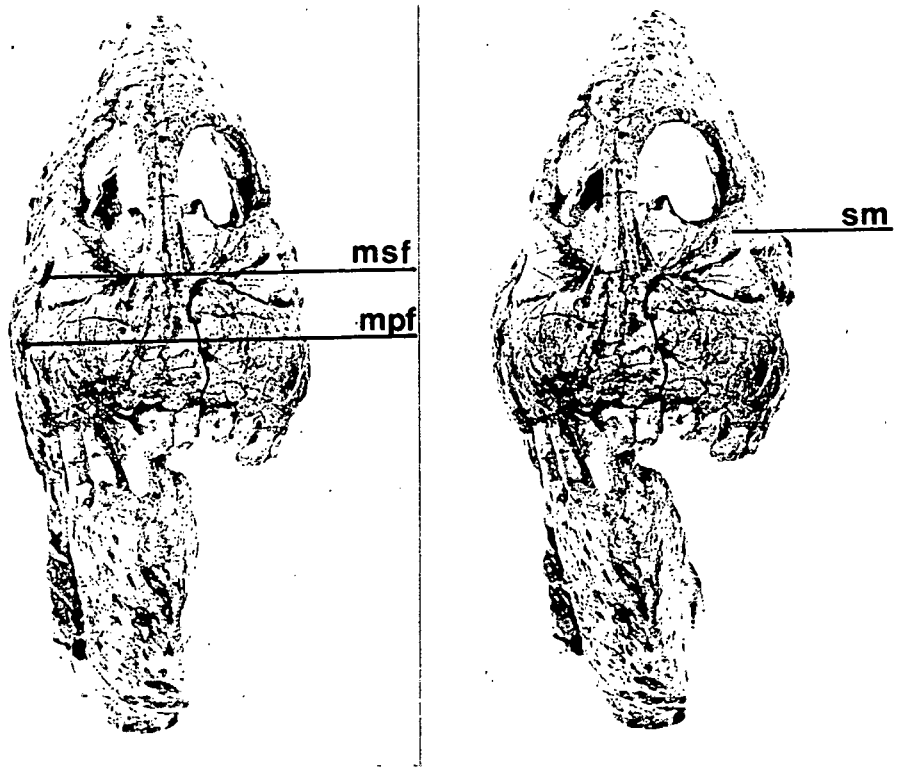

Fig. 50g Stereophotograph of *Glanosuchus macrops* GS M796. Anterior view of snout. Scale 20mm.

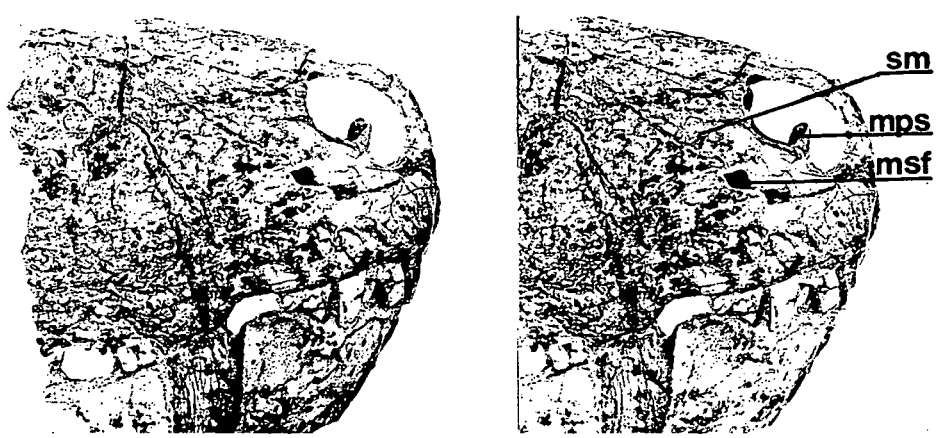

Fig. 50h Stereophotograph of *Glanosuchus macrops* GS M796. Right lateral view of snout. Scale 20mm.

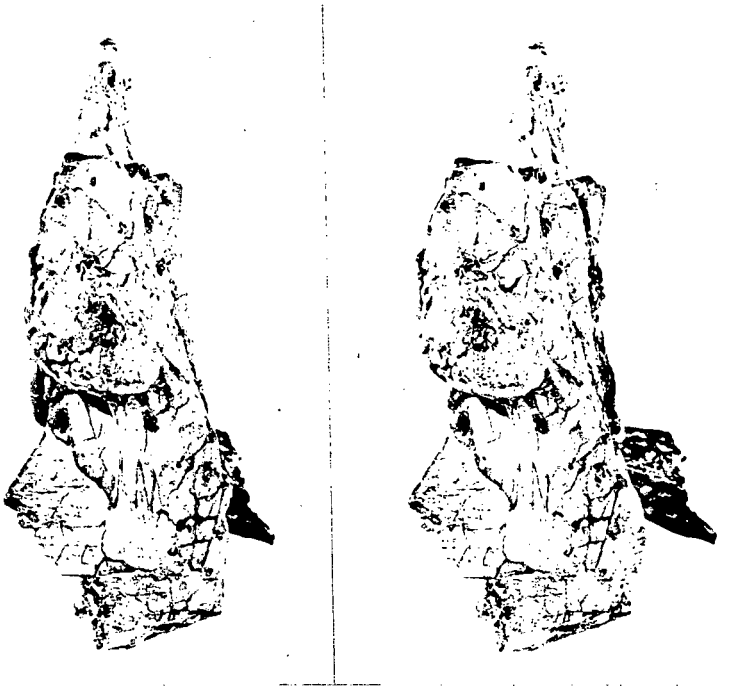

Fig. 50i Stereophotograph of *Glanosuchus macrops* GS M796. Right lateral view of skull roof. Scale 20mm.

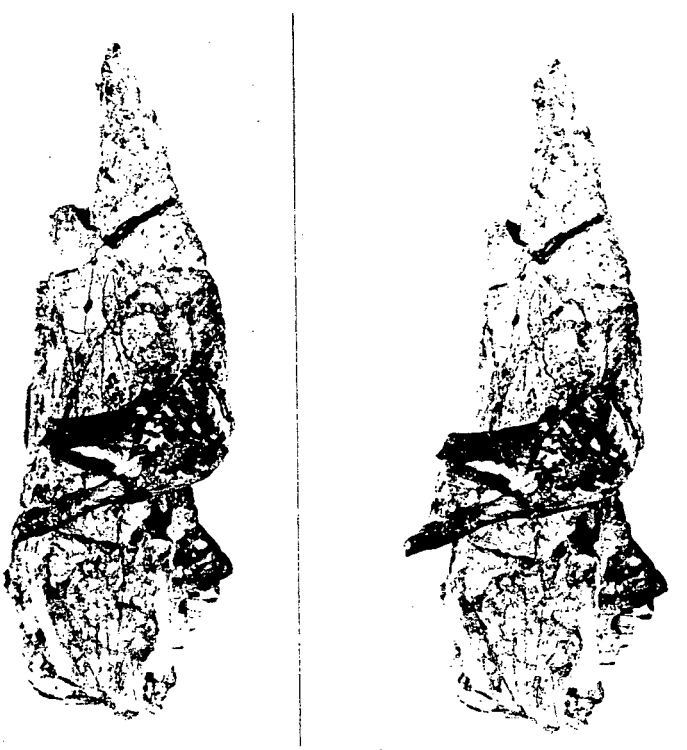

Fig. 50j Stereophotograph of *Glanosuchus macrops* GS M796. Left lateral view of skull roof. Scale 20mm.

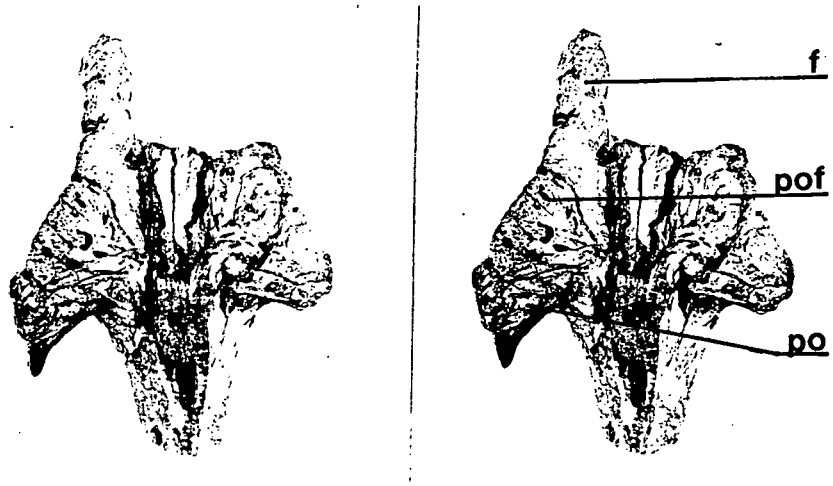

Fig. 50k Stereophotograph of *Glanosuchus macrops* GS M796. Dorsal view of skull roof. Scale 20mm.

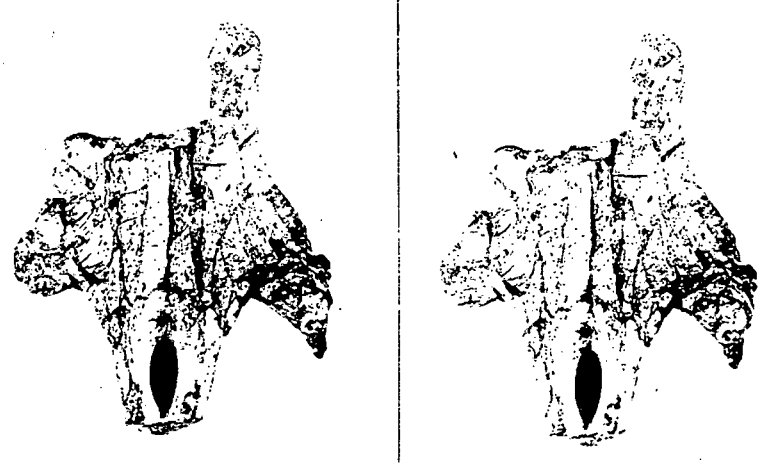

Fig. 50l Stereophotograph of *Glanosuchus macrops* GS M796. Ventral view of skull roof. Scale 20mm.

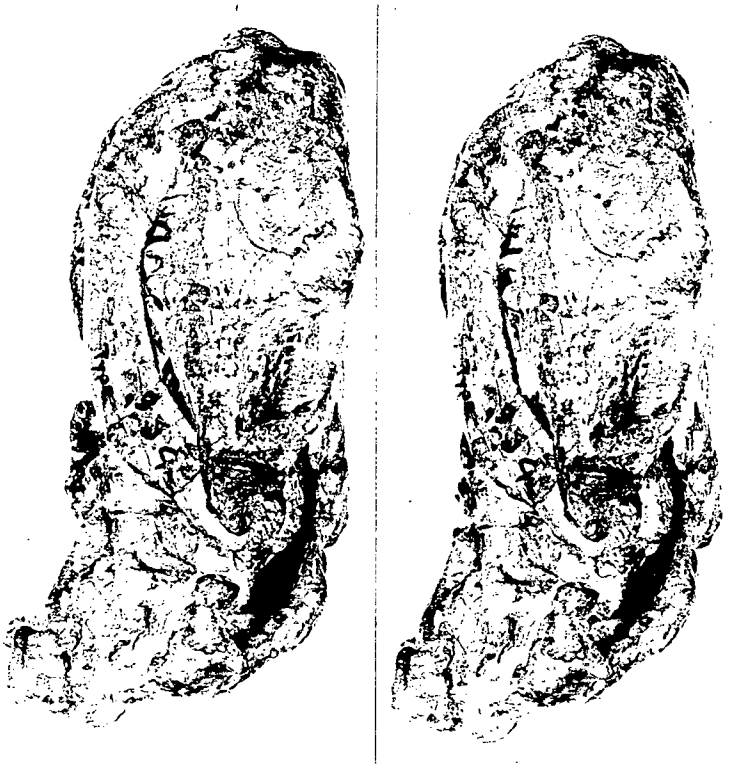

Fig. 51a Stereophotograph of the type skull of *Hofmeyria atavus* TM 245. Left lateral view. Scale 20mm.

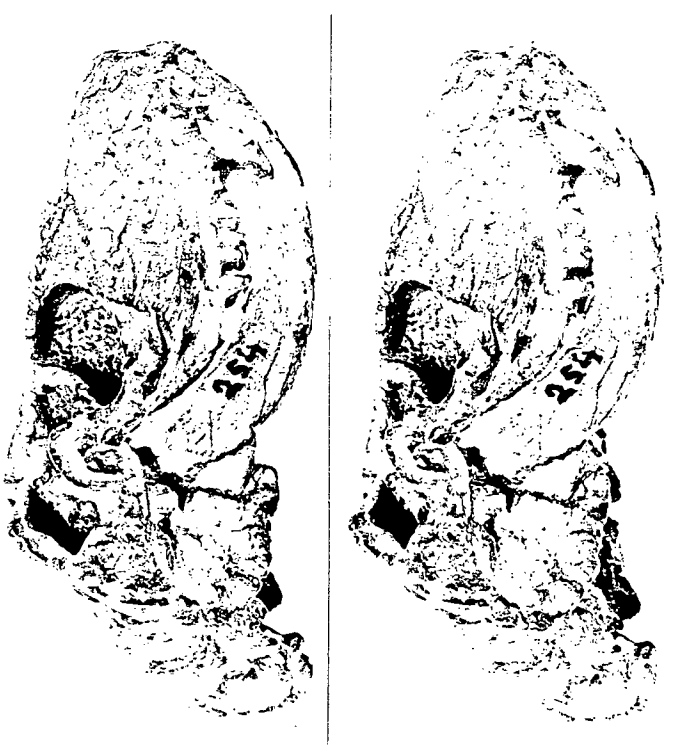

Fig. 51b Stereophotograph of the type skull of *Hofmeyria atavus* TM 254. Right lateral view. Scale 20mm.

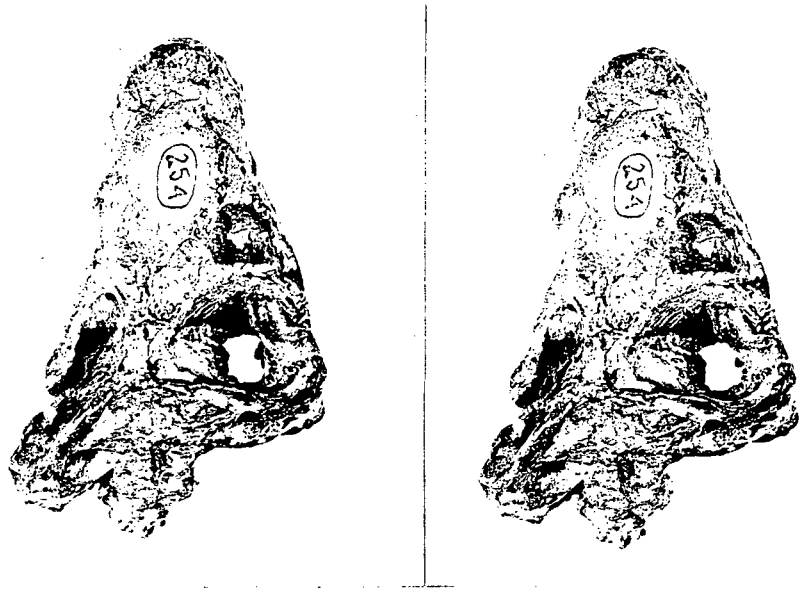

Fig. 51c Stereophotograph of the type skull of ***Hofmeyria atavus*** TM 254. Dorsal view. Scale 20mm.

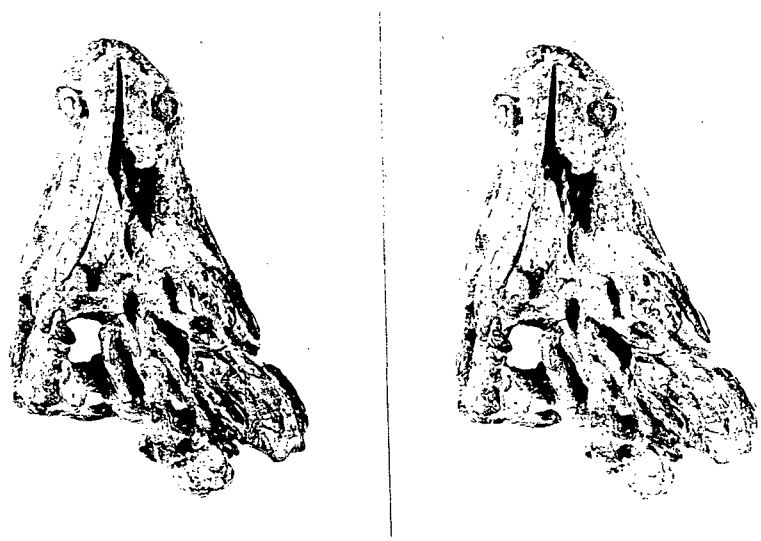

Fig. 51d Stereophotograph of the type skull of ***Hofmeyria atavus*** TM 254. Ventral view. Scale 20mm.

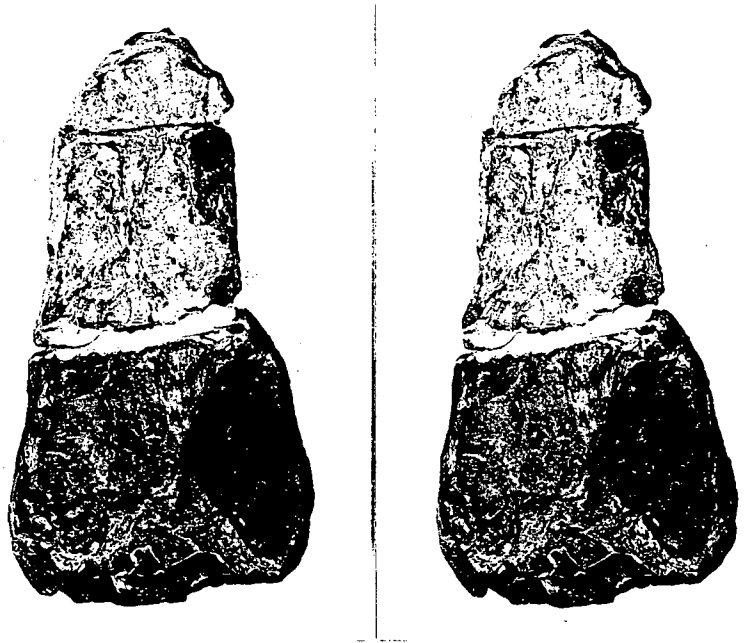

Fig. 52a Stereophotograph of the type skull of *Hyaenasuchus whaitsi* SAM 1079. Dorsal view. Scale 20mm.

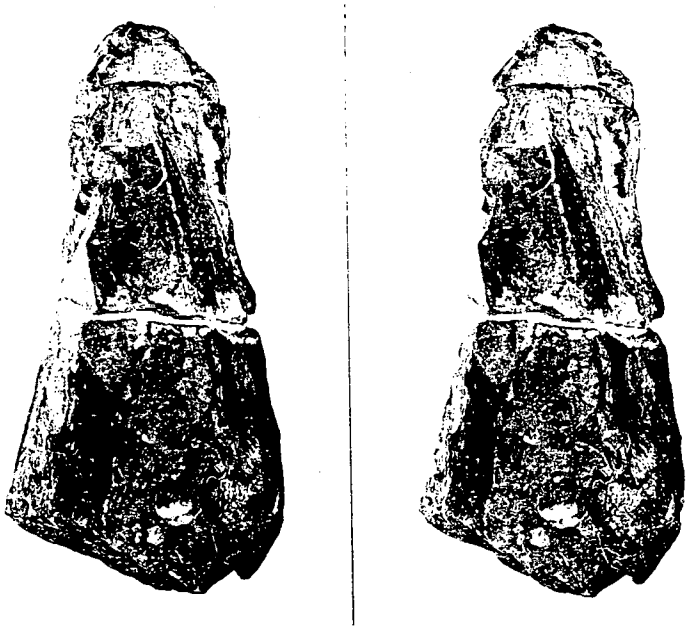

Fig. 52b Stereophotograph of the type skull of *Hyaenasuchus whaitsi* SAM 1079. Ventral view. Scale 20mm.

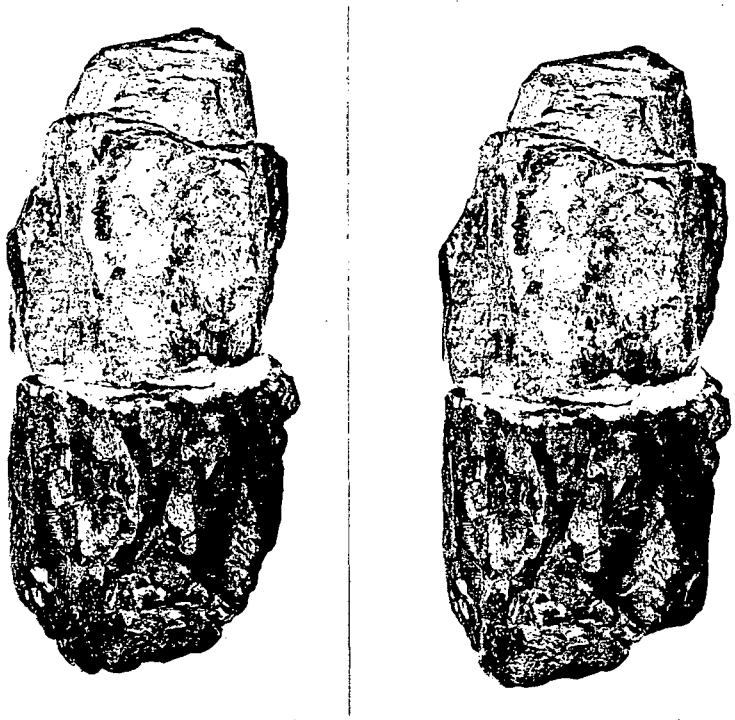

Fig. 52c Stereophotograph of the type skull of *Hyaenasuchus whaitsi* SAM 1079. Left lateral view. Scale 20mm.

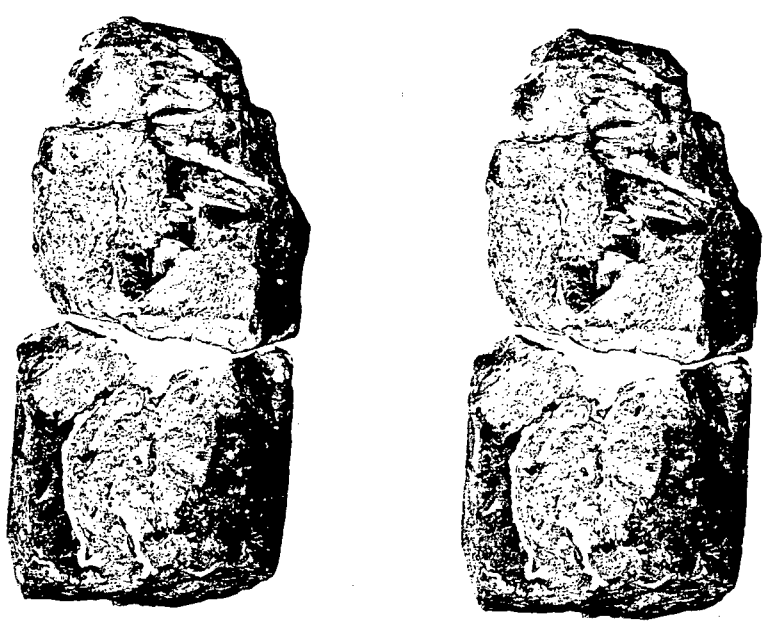

Fig. 52d Stereophotograph of the type skull of *Hyaenasuchus whaitsi* SAM 1079. Right lateral view. Scale 20mm.

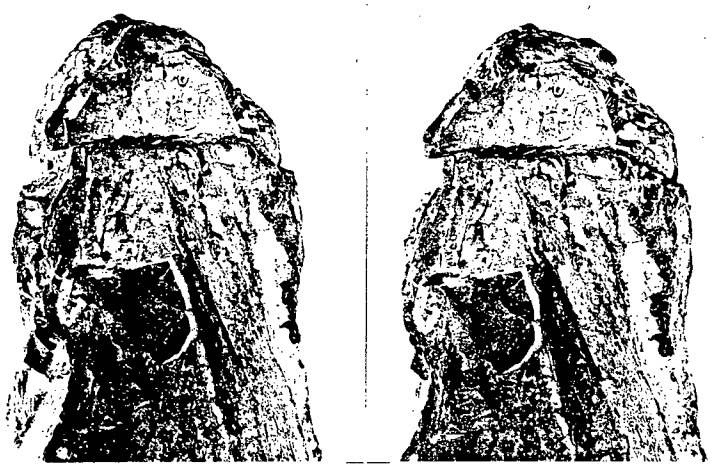

Fig. 52*e* Stereophotograph of the type skull of ***Hyaenasuchus whaitsi*** SAM 1079. Ventral view. Scale 20mm.

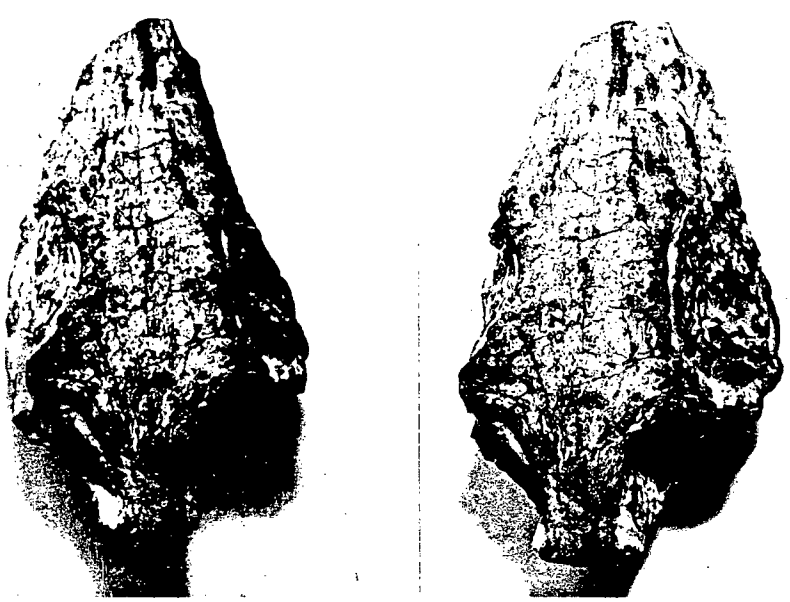

Fig. 53 Stereophotograph of the type of ***Hyorhynchus platyceps*** BMNH R872. Dorsal view. Scale 20mm.

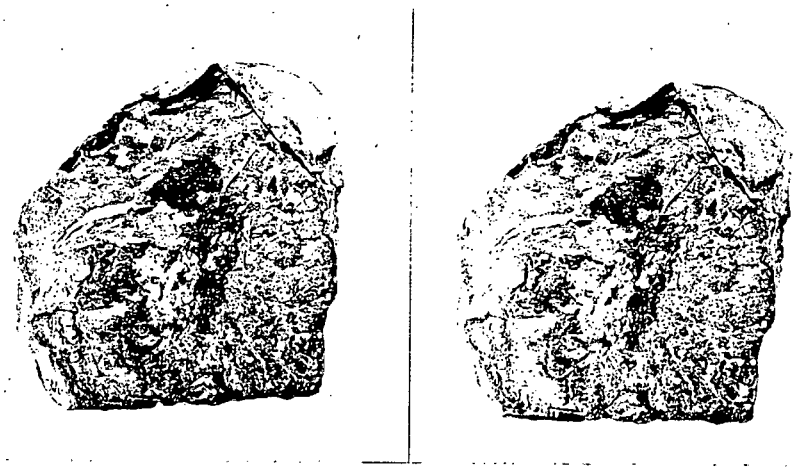

Fig. 54a Stereophotograph of the type of *Ictidosaurus angusticeps* SAM 630. Left lateral view. Scale 20mm.

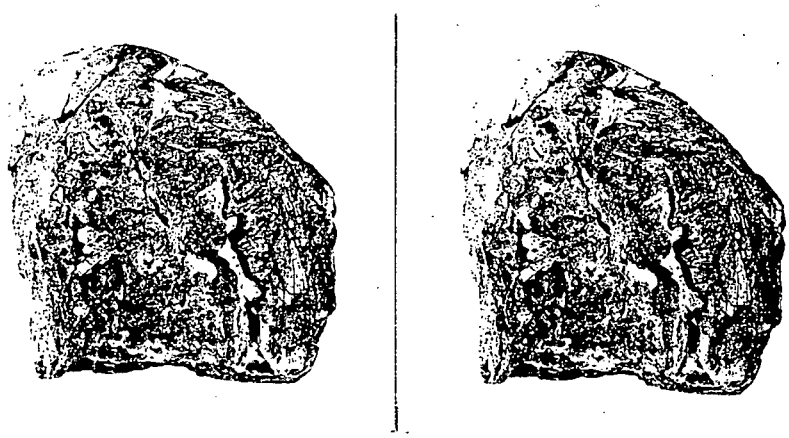

Fig. 54b Stereophotograph of the type of *Ictidosaurus angusticeps* SAM 630. Right lateral view. Scale 20mm.

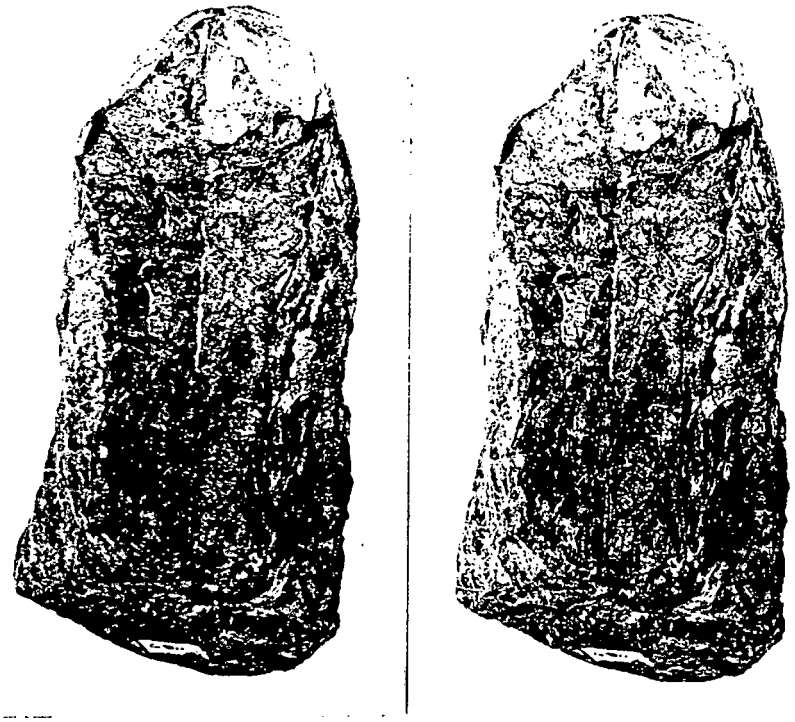

Fig. 54c Stereophotograph of the type of *Ictidosaurus angusticeps* SAM 630. Dorsal view. Scale 20mm.

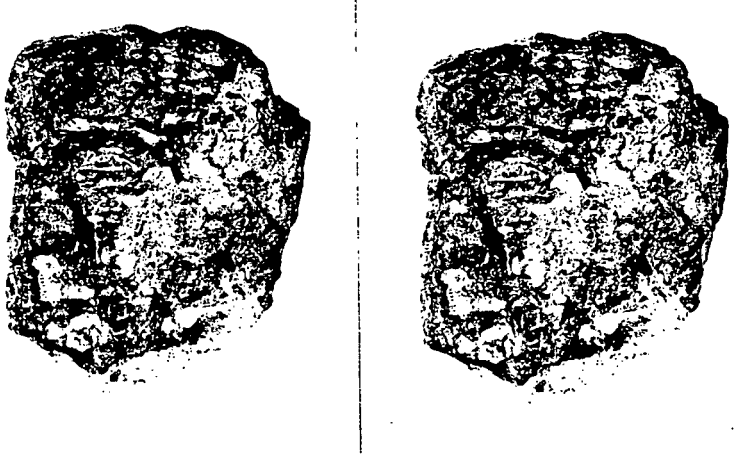

Fig. 55 Stereophotograph of *Ictidosaurus angusticeps* AMNH 5527. Left lateral view. Scale 20mm.

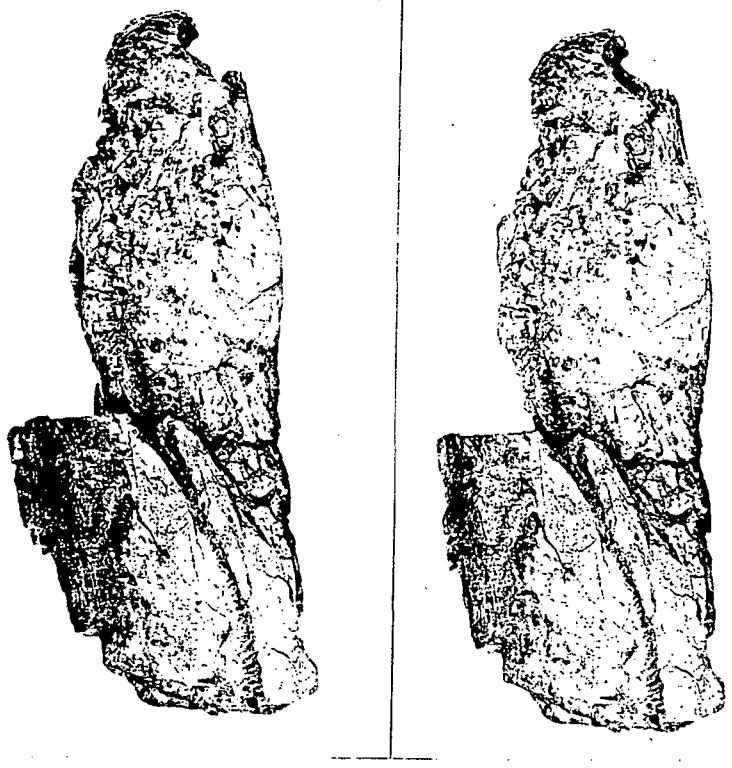

Fig. 56a Stereophotograph of the type skull of *Karoowalteria skinneri* BPI 220. Left lateral view. Scale 20mm.

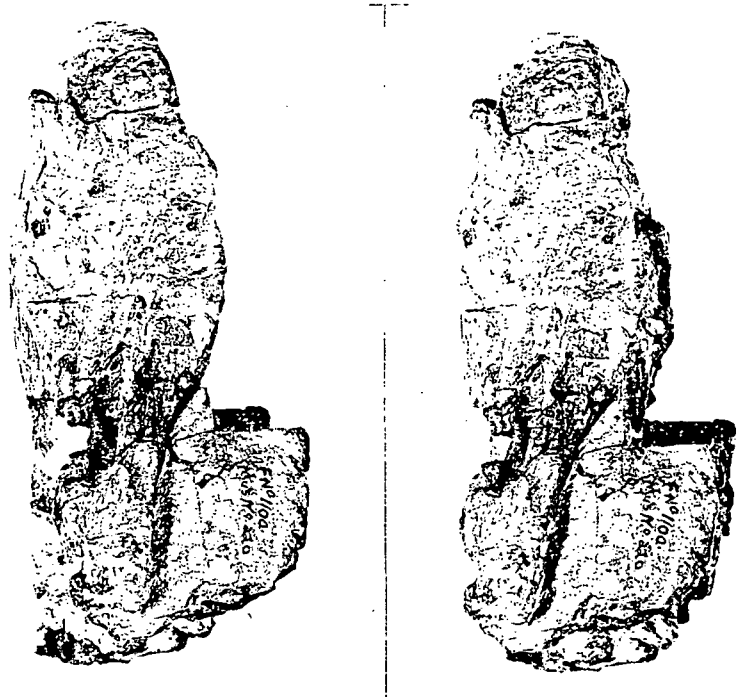

Fig. 56b Stereophotograph of the type skull of *Karoowalteria skinneri* BPI 220. Right lateral view. Scale 20mm.

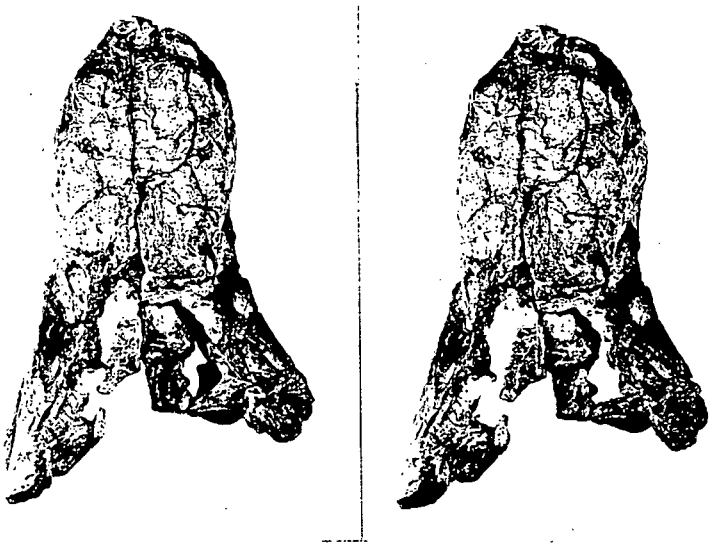

Fig. 56c Stereophotograph of the type skull of *Karoowalteria skinneri* BPI 220. Dorsal view. Scale 20mm.

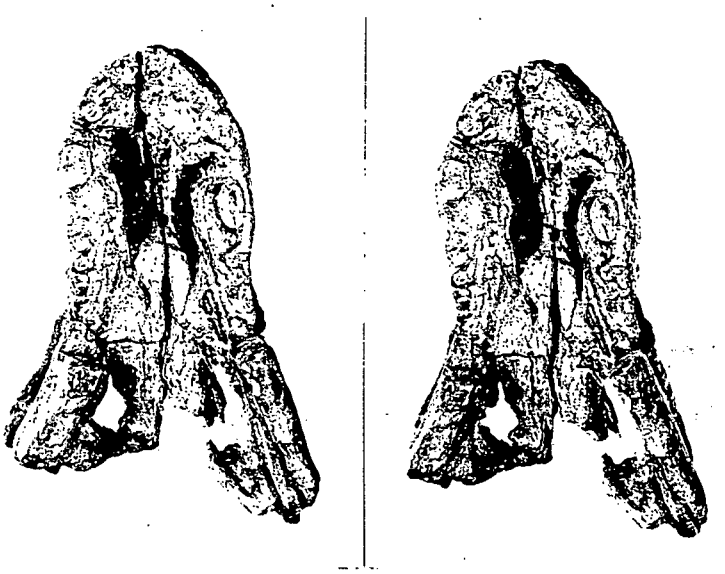

Fig. 56d Stereophotograph of the type skull of *Karoowalteria skinneri* BPI 220. Ventral view. Scale 20mm.

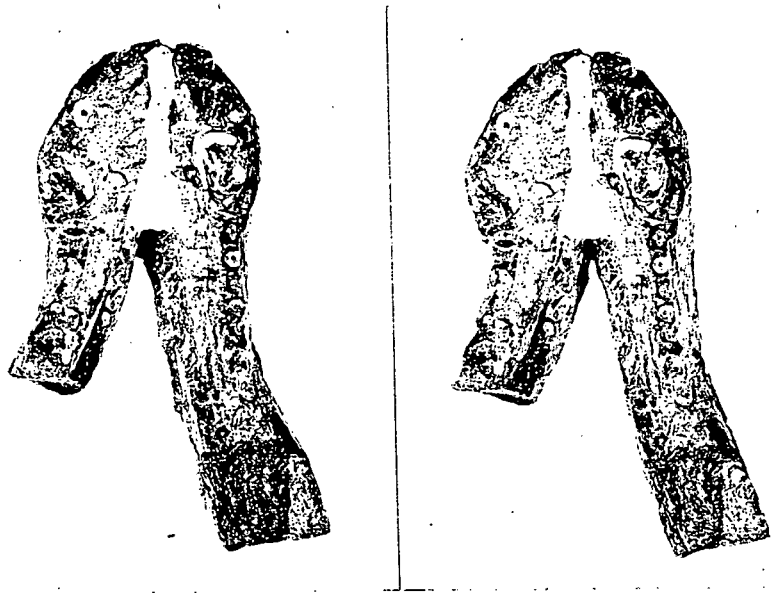

Fig. 56e Stereophotograph of the lower jaw of the type skull of *Karoowalteria skinneri* BPI 220. Dorsal view. Scale 20mm.

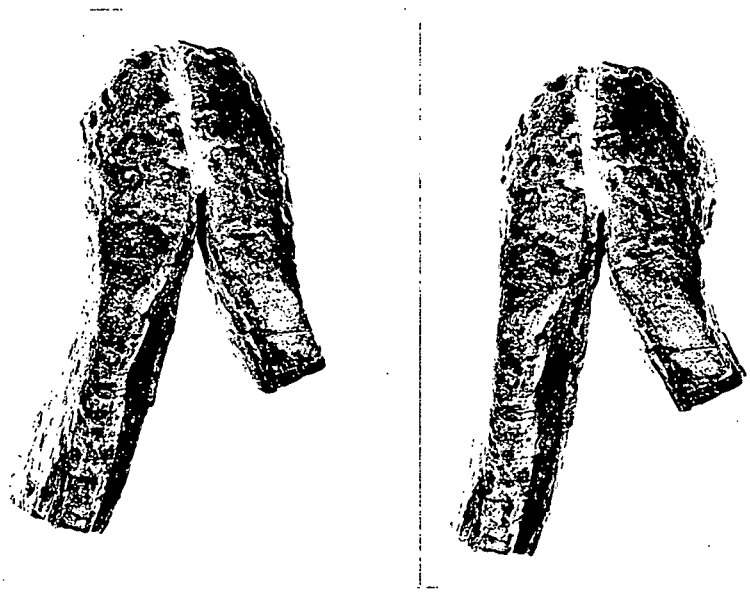

Fig. 56f Stereophotograph of the lower jaw of the type skull of *Karoowalteria skinneri* BPI 220. Ventral view. Scale 20mm.

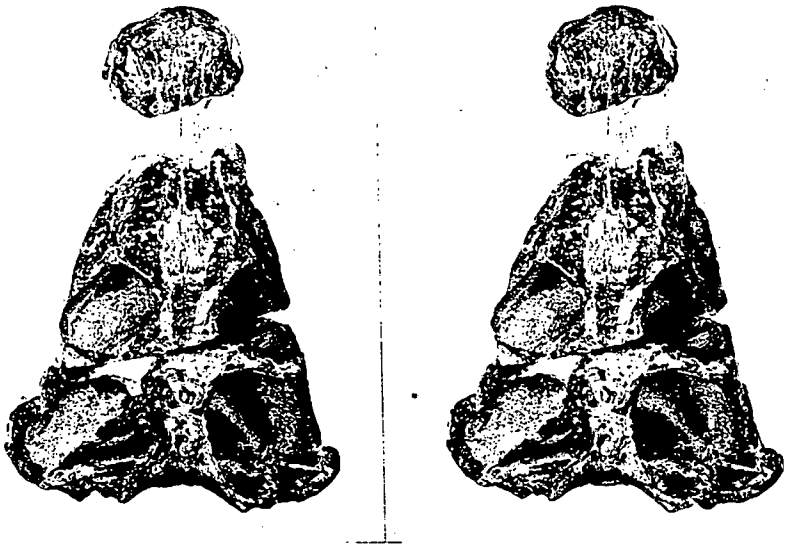

Fig. 57a Stereophotograph of the type skull of *Lycedops scholtzi* MM 4499. Dorsal view. Scale 20mm.

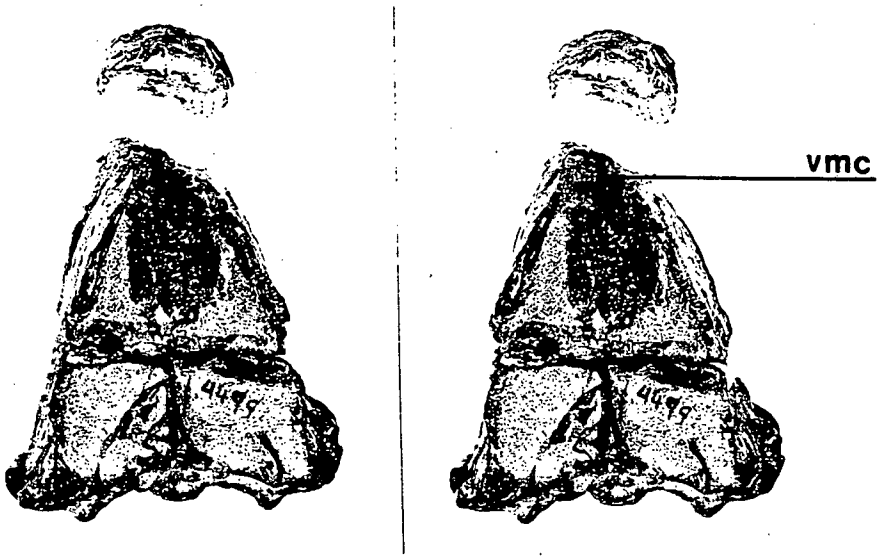

Fig. 57b Stereophotograph of the type skull of *Lycedops scholtzi* MM 4499. Ventral view. Scale 20mm.

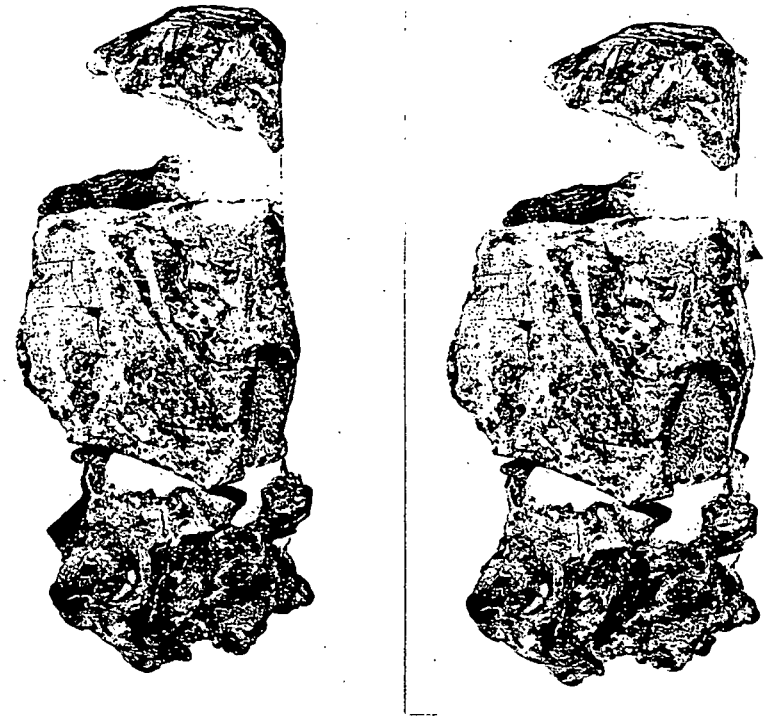

Fig. 57c Stereophotograph of the type skull of *Lycedops scholtzi* MM 4499.

Left lateral view. Scale 20mm.

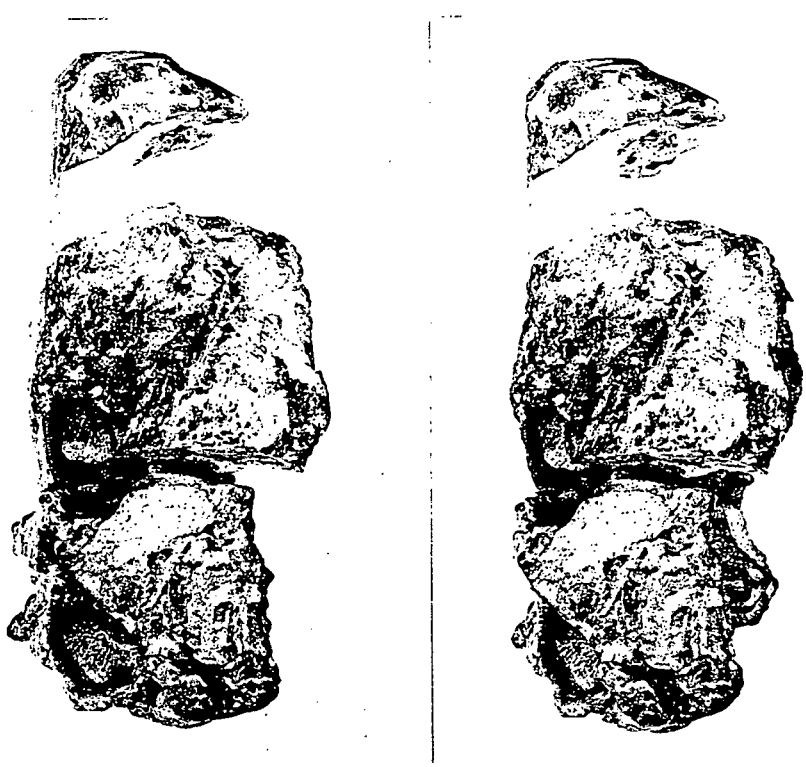

Fig. 57d Stereophotograph of the type skull of *Lycedops scholtzi* MM 4499.

Right lateral view. Scale 20mm.

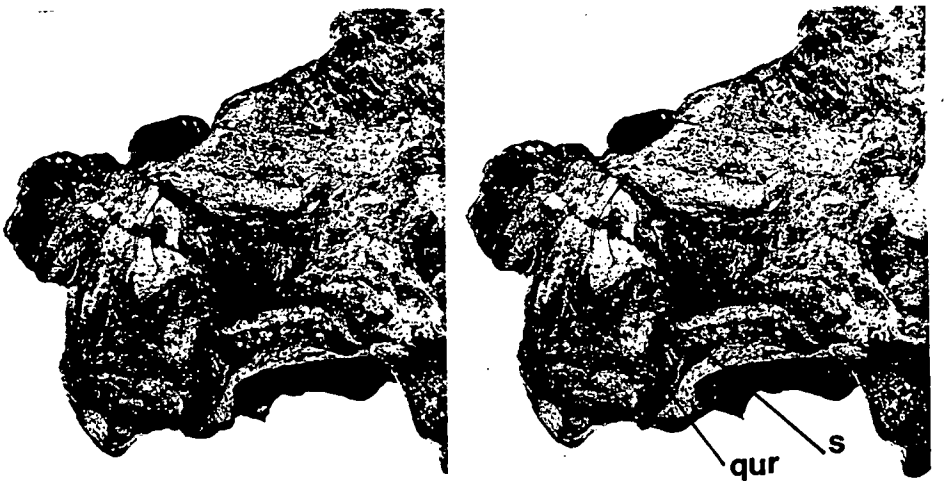

Fig. 57e Stereophotograph of the type skull of *Lycedops scholtzi* MM 4499. Left occipital view. Scale 20mm.

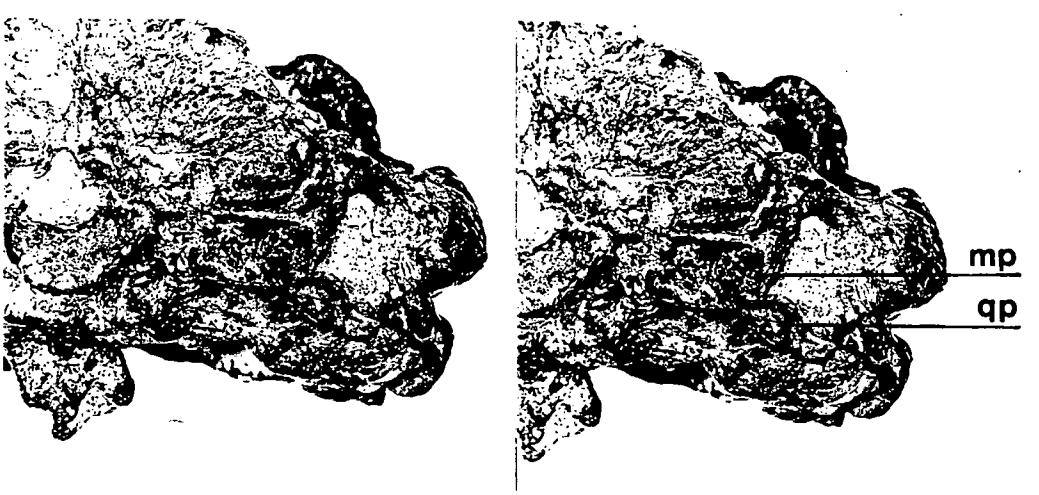

Fig. 57f Stereophotograph of the type skull of *Lycedops scholtzi* MM 4499. Right occipital view. Scale 20mm.

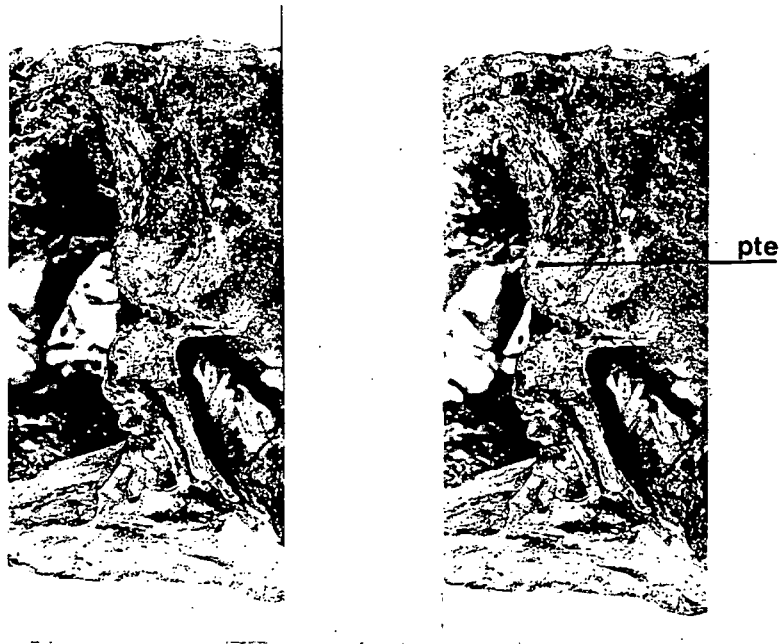

Fig. 57g Stereophotograph of the type skull of *Lycedops scholtzi* NM 4499. Transverse section through interpterygoid vacuity. Scale 20mm.

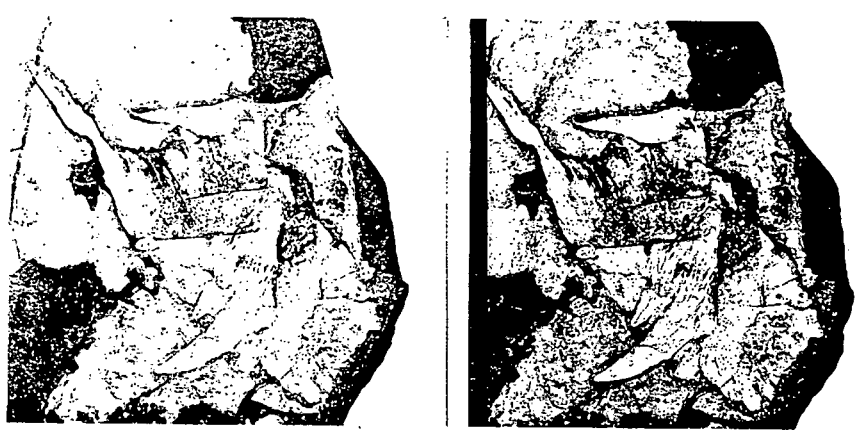

Fig. 58 Stereophotograph of the type of *Lycosuchus mackayi* SAM 633. Lateral view of maxilla. Scale 20mm.

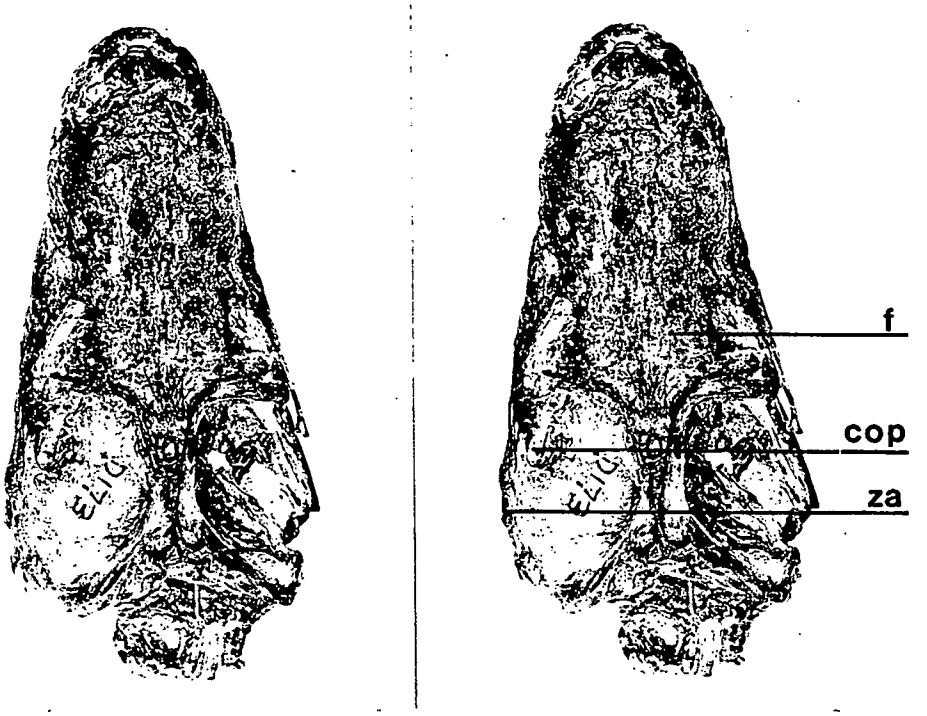

Fig. 59a Stereophotograph of the type skull of *Lycosuchus vanderrieti* US D173. Dorsal view. Scale 20mm.

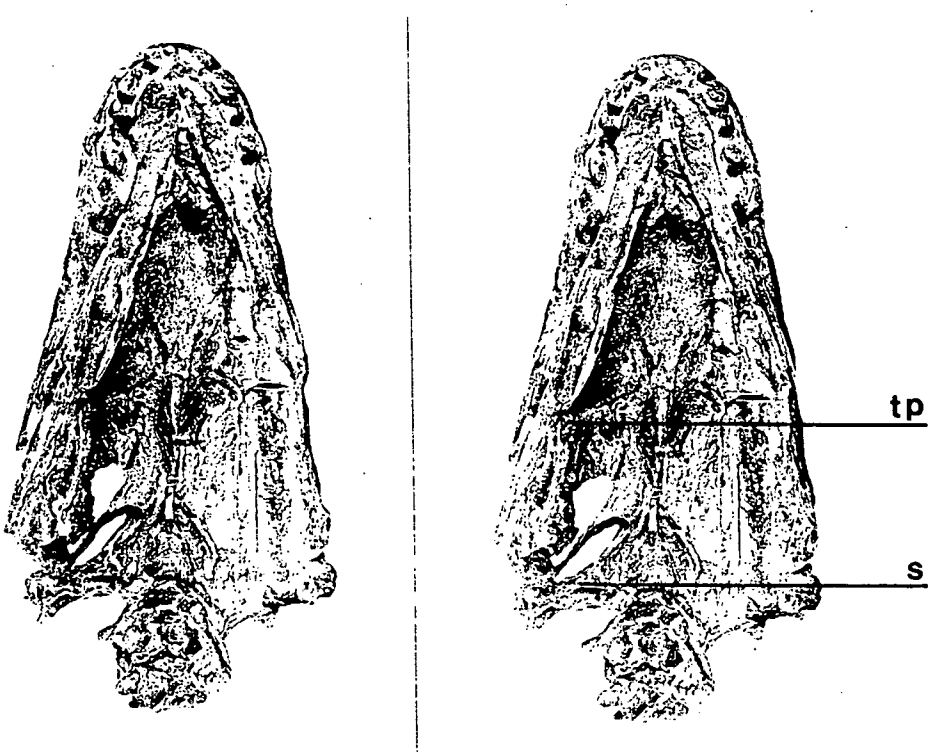

Fig. 59b Stereophotograph of the type skull of *Lycosuchus vanderrieti* US D173. Ventral view. Scale 20mm.

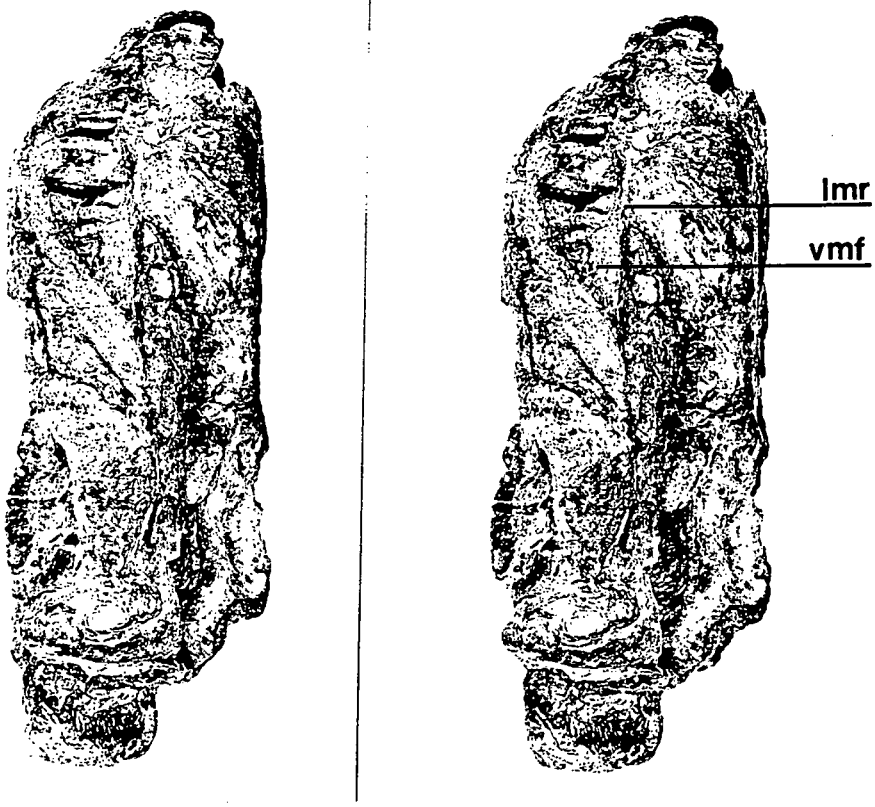

Fig. 59c Stereophotograph of the type skull of *Lycosuchus vanderrieti* US D173. Left lateral view. Scale 20mm.

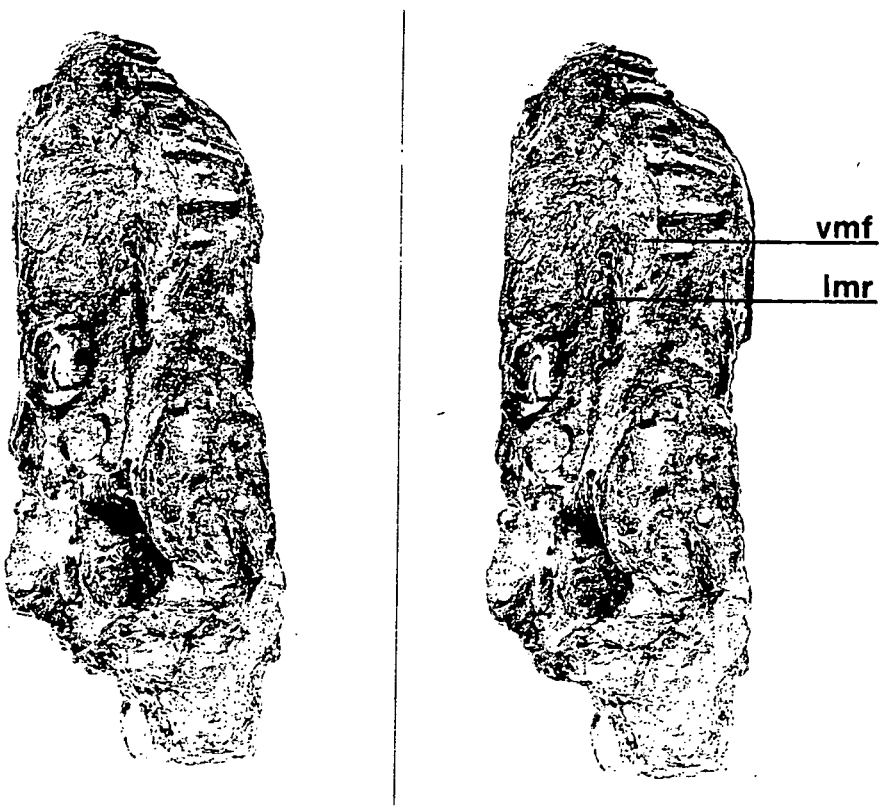

Fig. 59d Stereophotograph of the type skull of *Lycosuchus vanderrieti* US D173. Right lateral view. Scale 20mm.

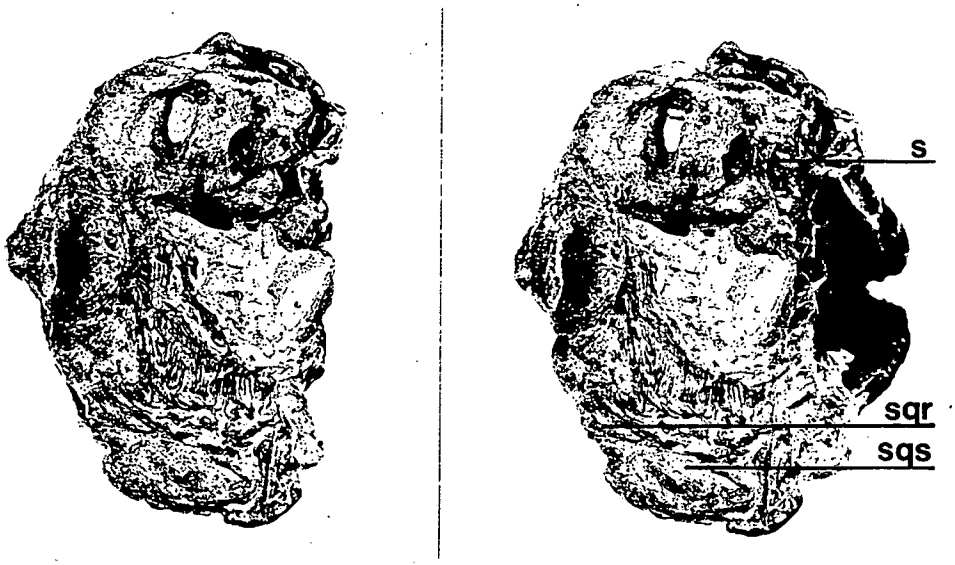

Fig. 59e Stereophotograph of the type skull of *Lycosuchus vanderrieti* US D173. Occipital view. Scale 20mm.

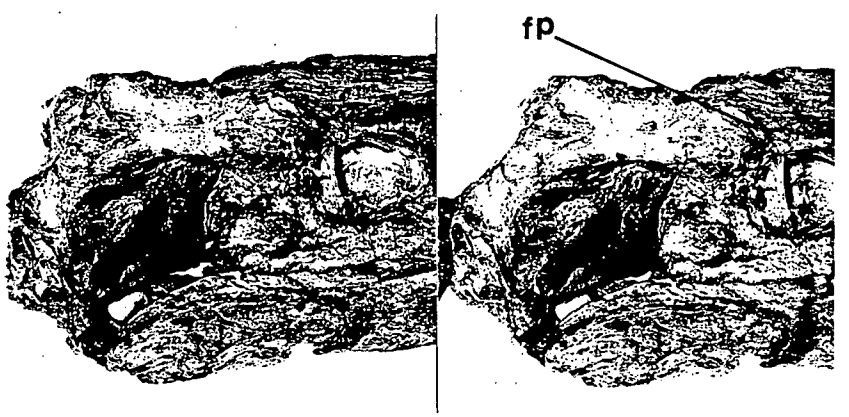

Fig. 59f Stereophotograph of the type skull of *Lycosuchus vanderrieti* US D173. Dorsolateral view of right postorbital region. Scale 20mm.

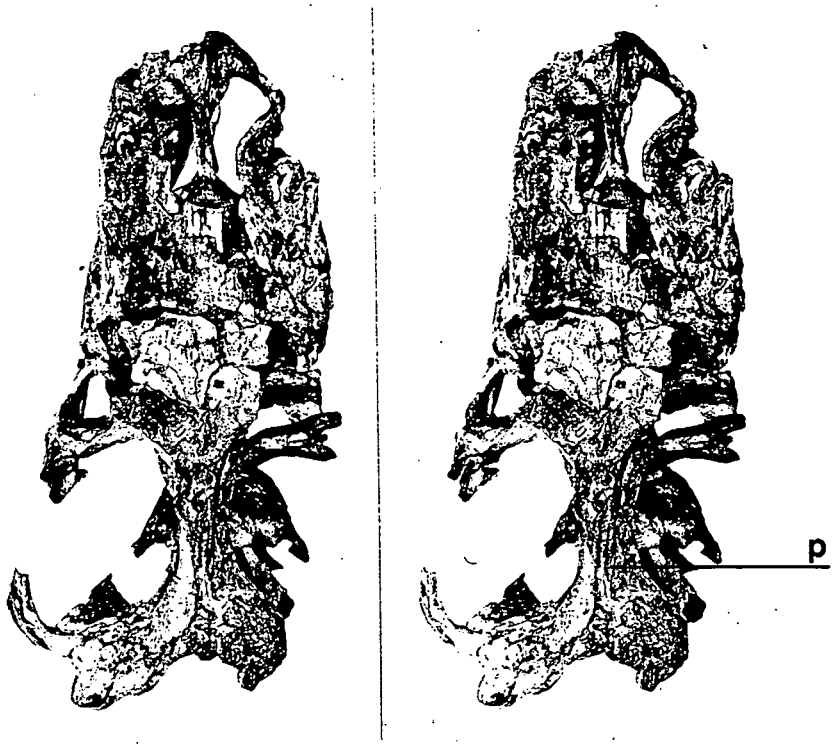

Fig. 60a Stereophotograph of *Lycosuchus vanderrieti* GS M793. Dorsal view of skull. Scale 20mm.

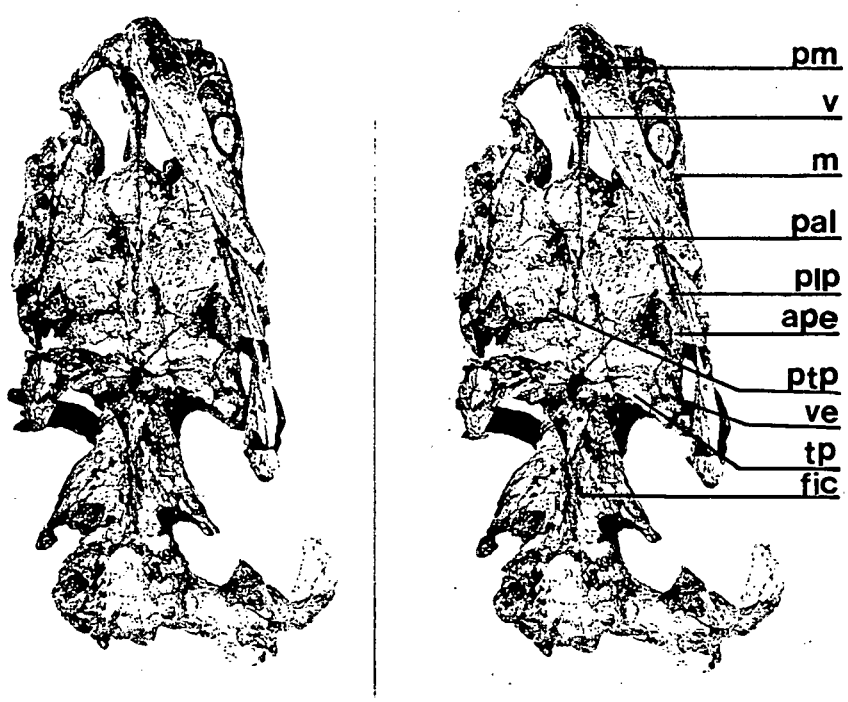

Fig. 60b Stereophotograph of *Lycosuchus vanderrieti* GS M793. Ventral view of skull. Scale 20mm.

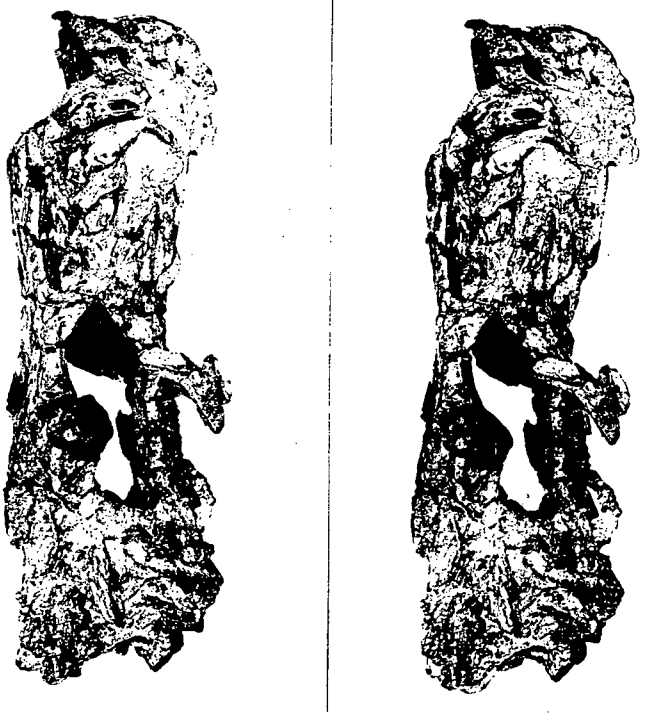

Fig. 60c Stereophotograph of *Lycosuchus vanderrieti* GS M793. Right lateral view of skull. Scale 20mm.

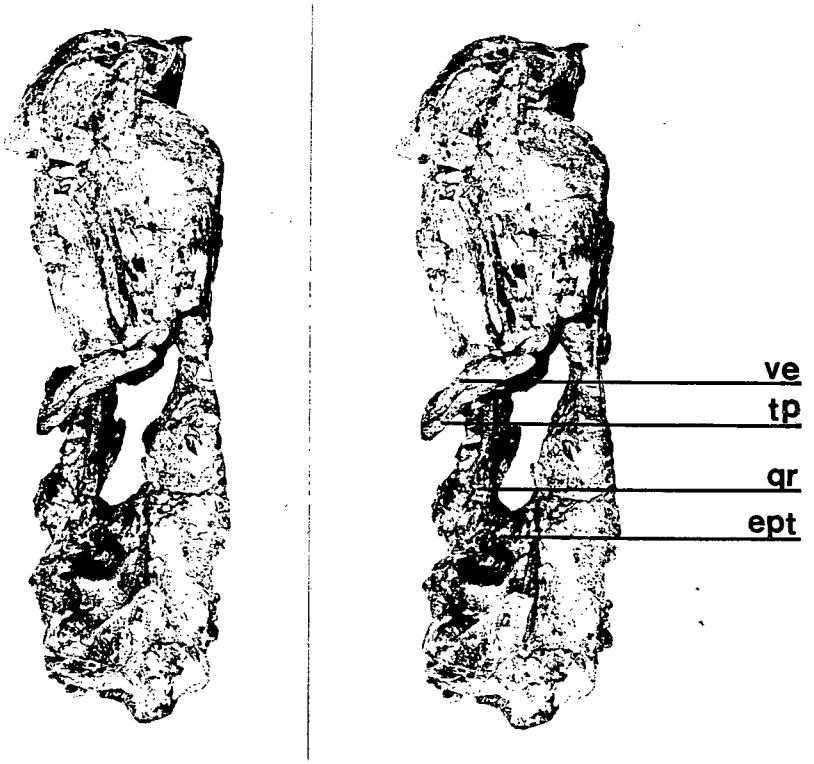

Fig. 60d Stereophotograph of *Lycosuchus vanderrieti* GS M793. Left lateral view of skull. Scale 20mm.

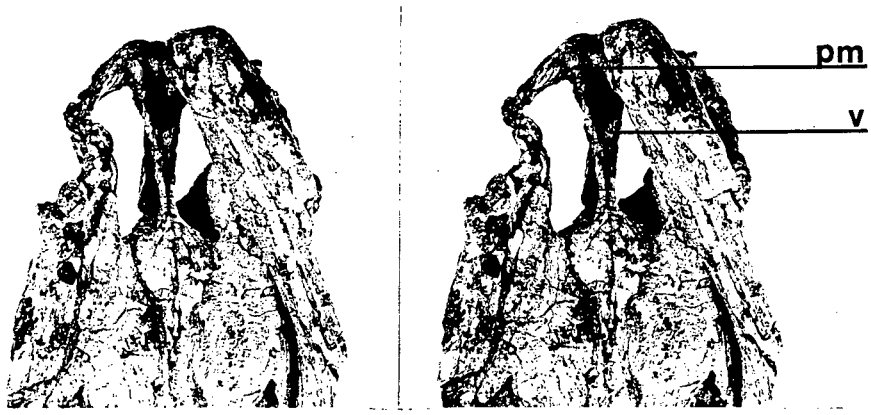

Fig. 60e Stereophotograph of *Lycosuchus vanderrieti* GS M793. Ventral view of palate. Scale 20mm.

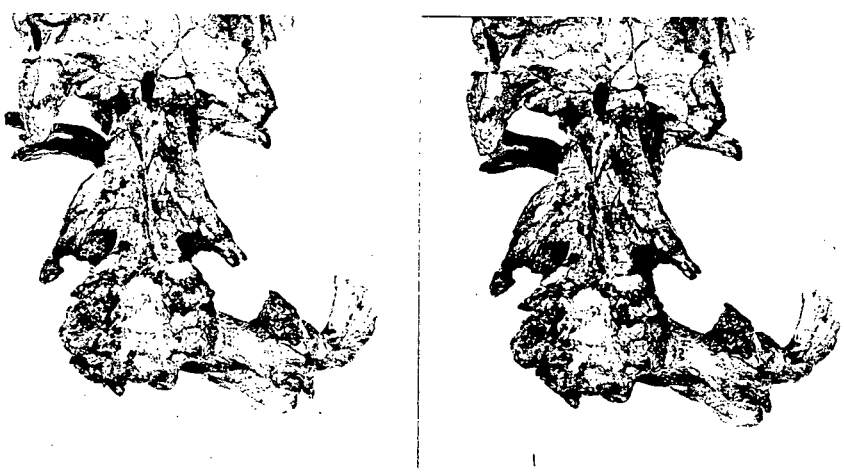

Fig. 60f Stereophotograph of *Lycosuchus vanderrieti* GS M793. Ventral view of skull base. Scale 20mm.

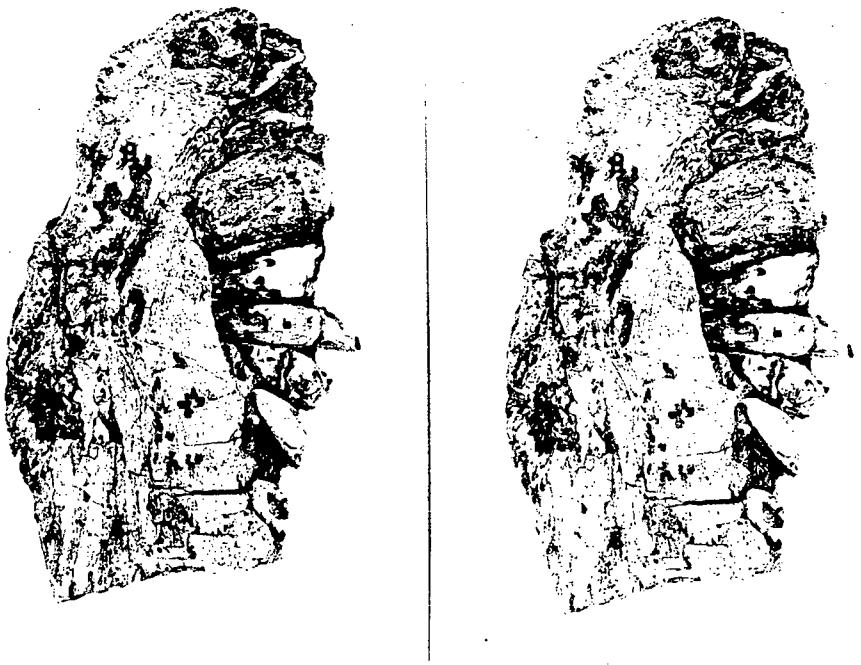

Fig. 60g Stereophotograph of *Lycosuchus vanderrieti* GS M793. Medial view of anterior portion of right jaw ramus. Scale 20mm.

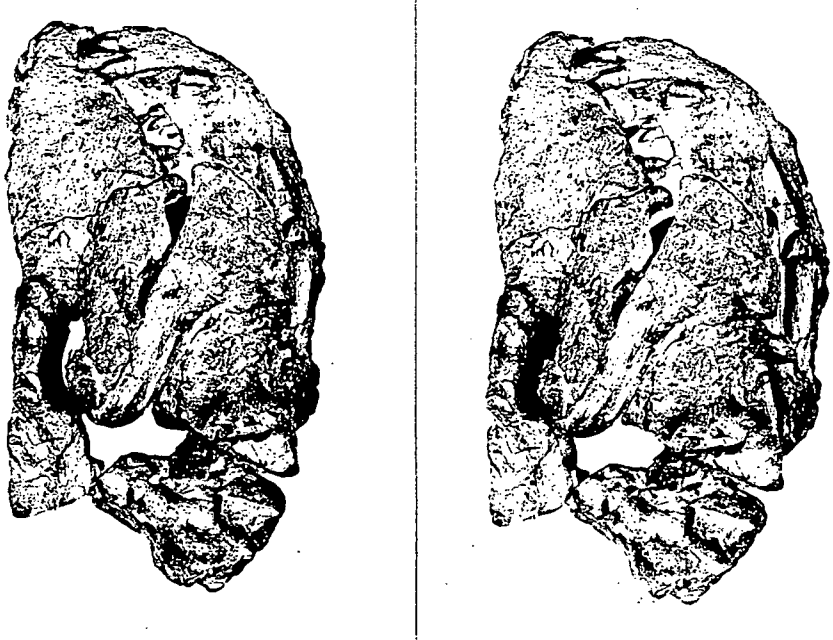

Fig. 61a Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Right lateral view of skull. Scale 20mm.

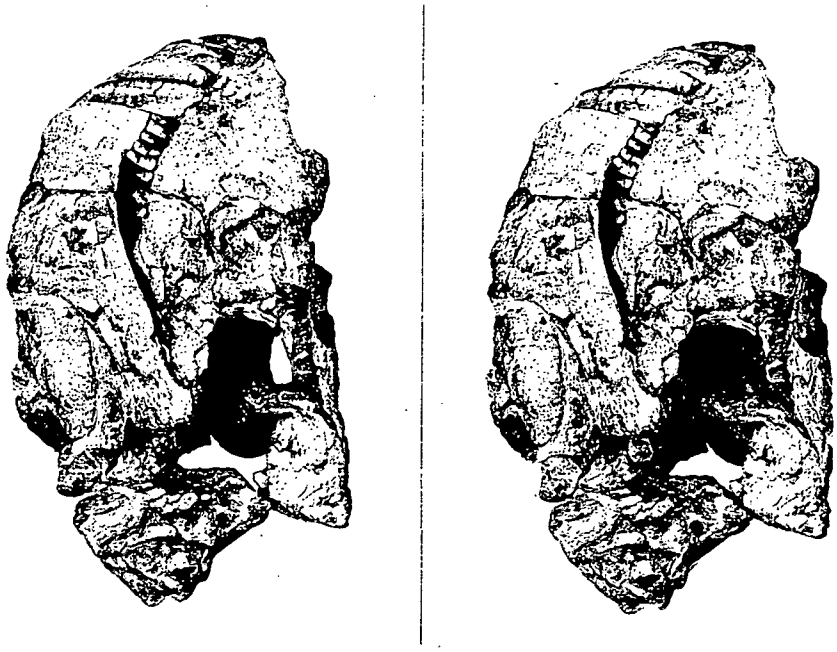

Fig. 61b Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Left lateral view of skull. Scale 20mm.

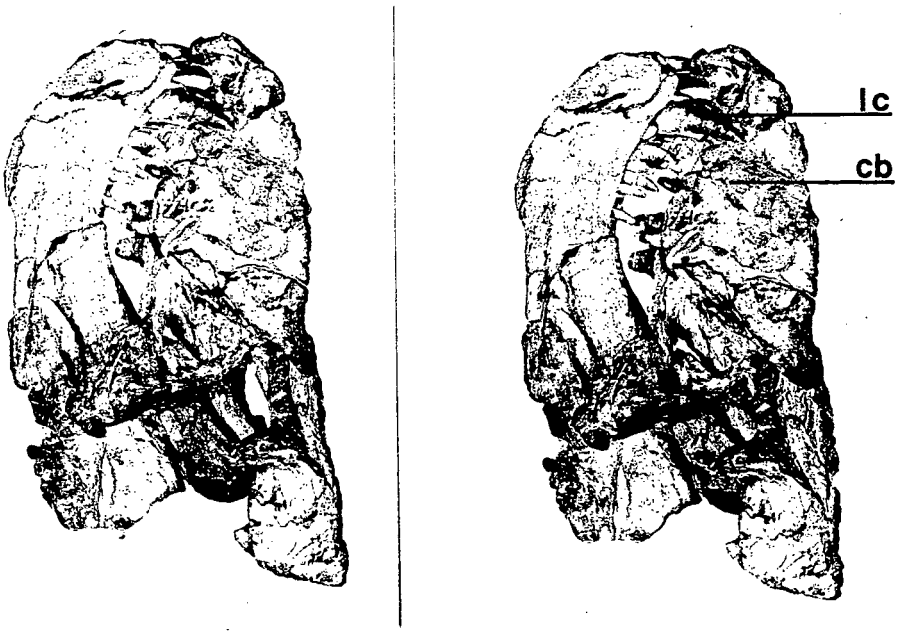

Fig. 61c Stereophotograph of the type of *Lycosuchus keyseri* GS C60.
Medial view of right half of skull and lower jaw. Scale 20mm.

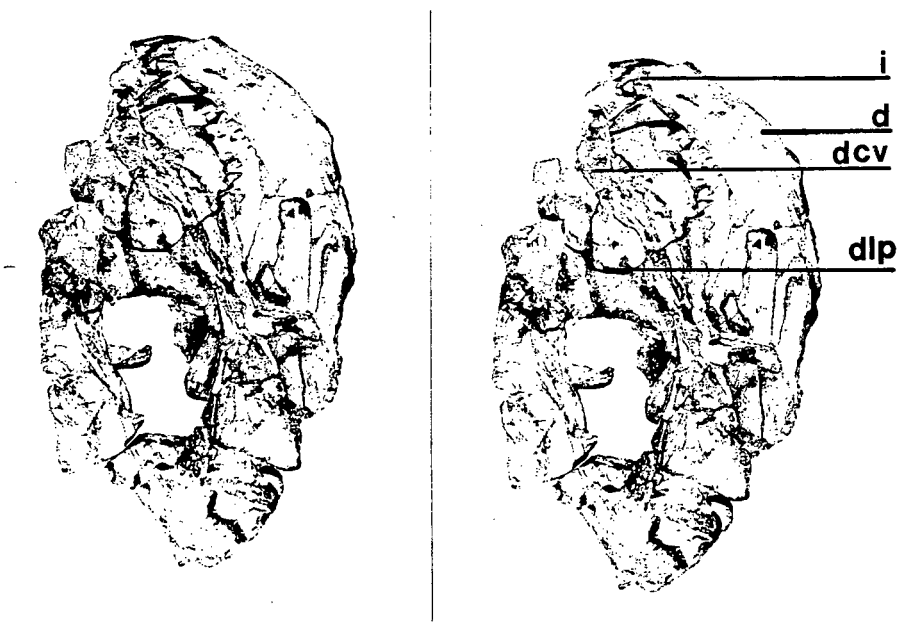

Fig. 61d Stereophotograph of the type of *Lycosuchus keyseri* GS C60
Medial view of left half of skull and lower jaw. Scale 20mm.

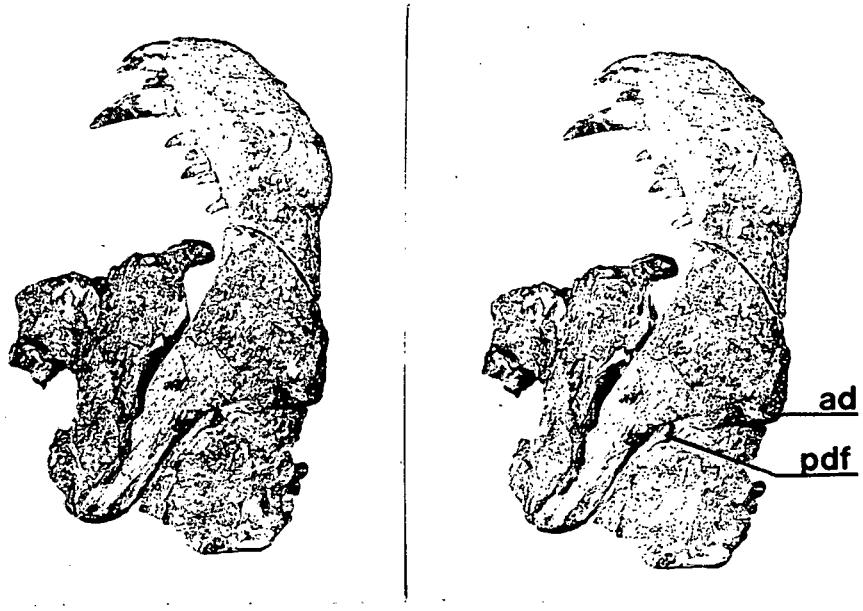

Fig. 61e Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Lateral view of right lower jaw ramus. Scale 20mm.

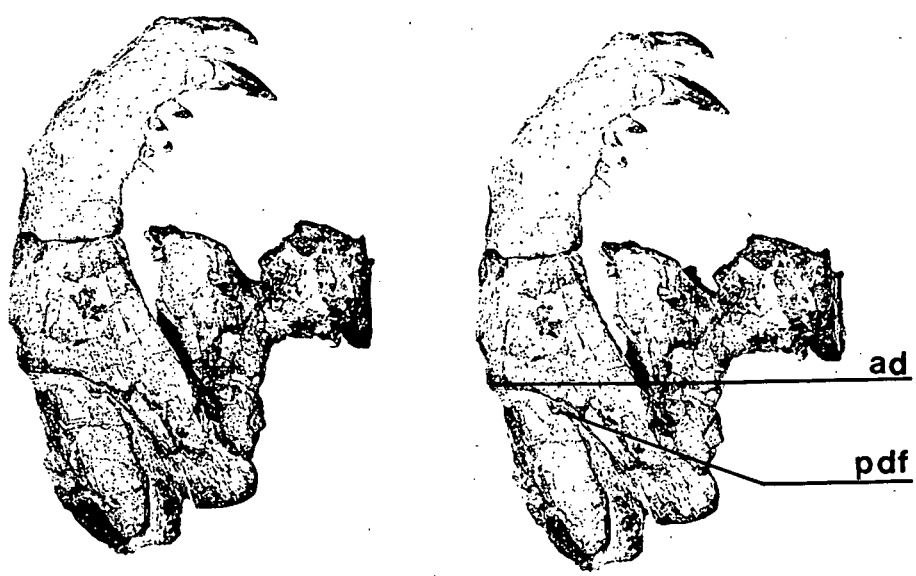

Fig. 61f Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Lateral view of left lower jaw ramus. Scale 20mm.

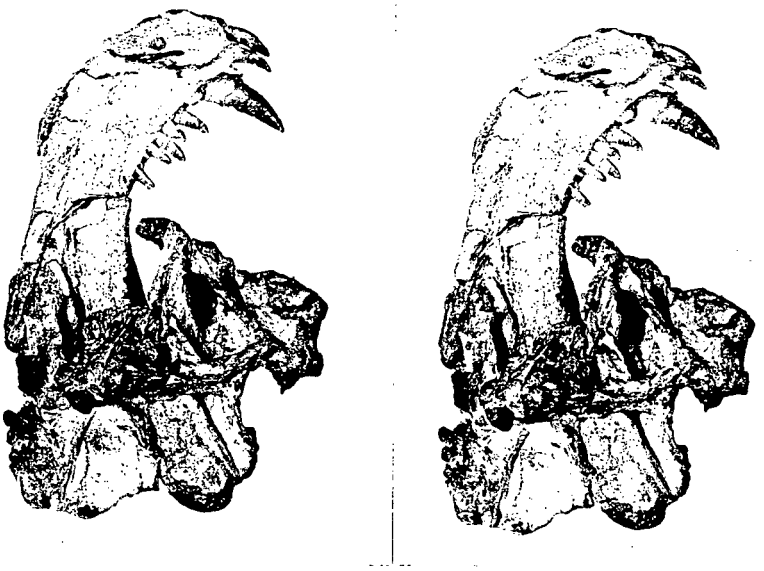

Fig. 61g Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Medial view of right lower jaw ramus. Scale 20mm.

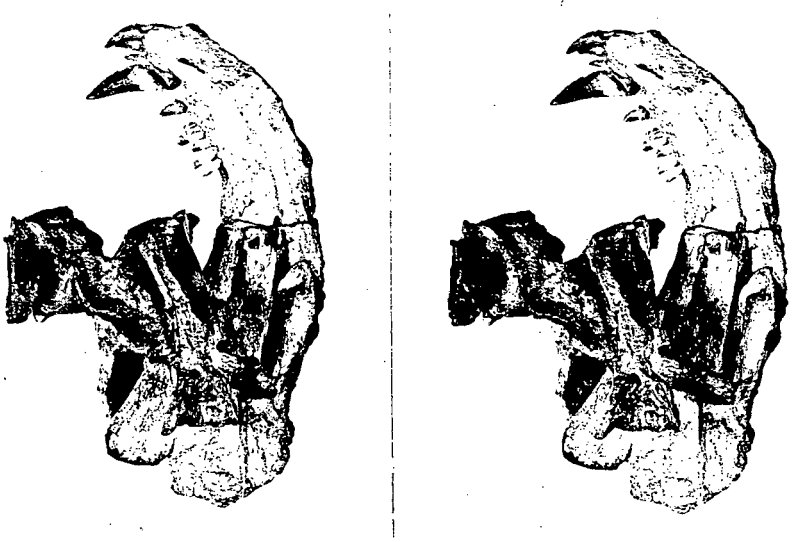

Fig. 61h Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Medial view of left lower jaw ramus. Scale 20mm.

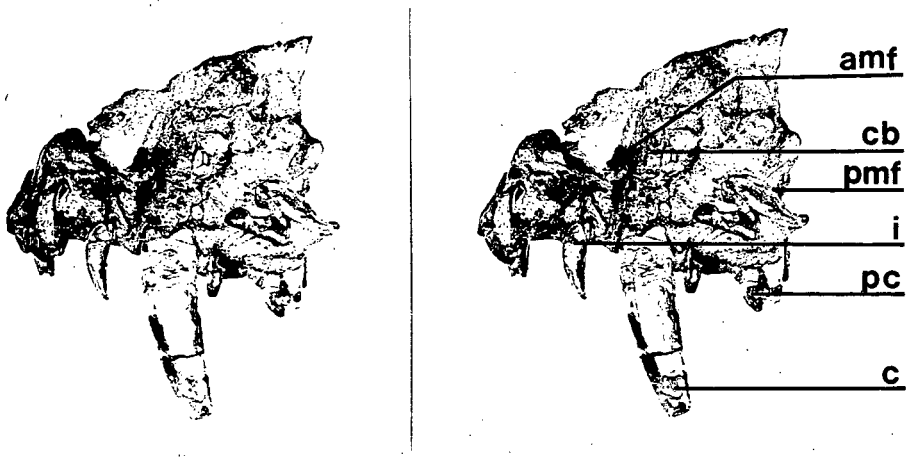

Fig. 61i Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Medial view of right maxilla and premaxilla. Scale 20mm.

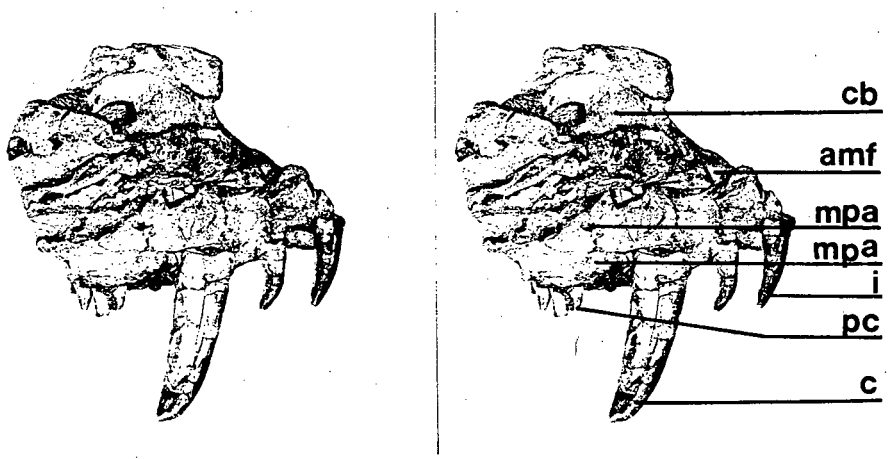

Fig. 61j Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Medial view of left maxilla and premaxilla. Scale 20mm.

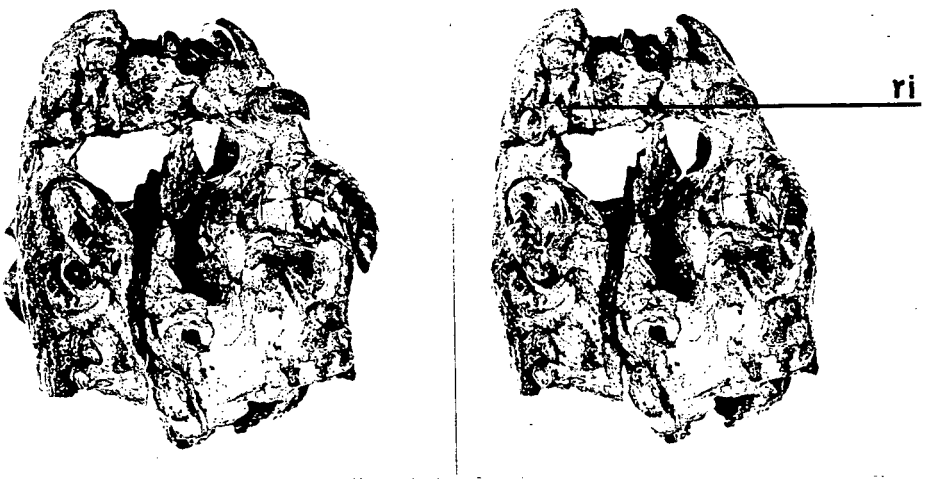

Fig. 61k Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Ventral view of anterior part of snout. Scale 20mm.

Fig. 61l Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Anterior view of braincase. Scale 20mm.

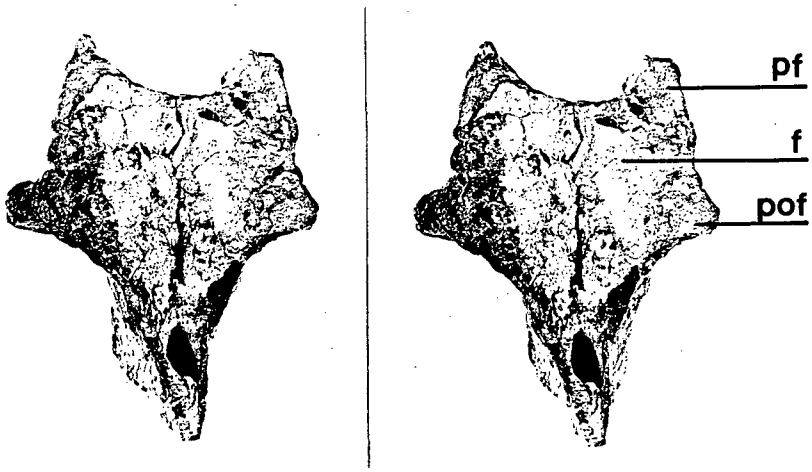

Fig. 61m Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Dorsal view of skull roof. Scale 20mm.

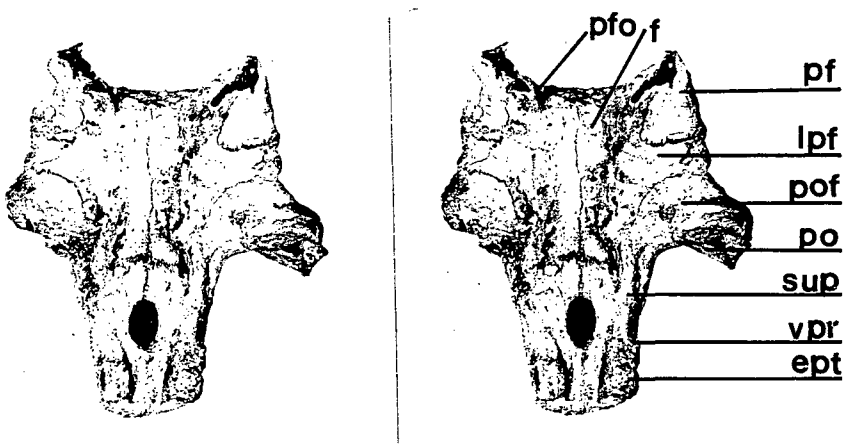

Fig. 61n Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Ventral view of skull roof. Scale 20mm.

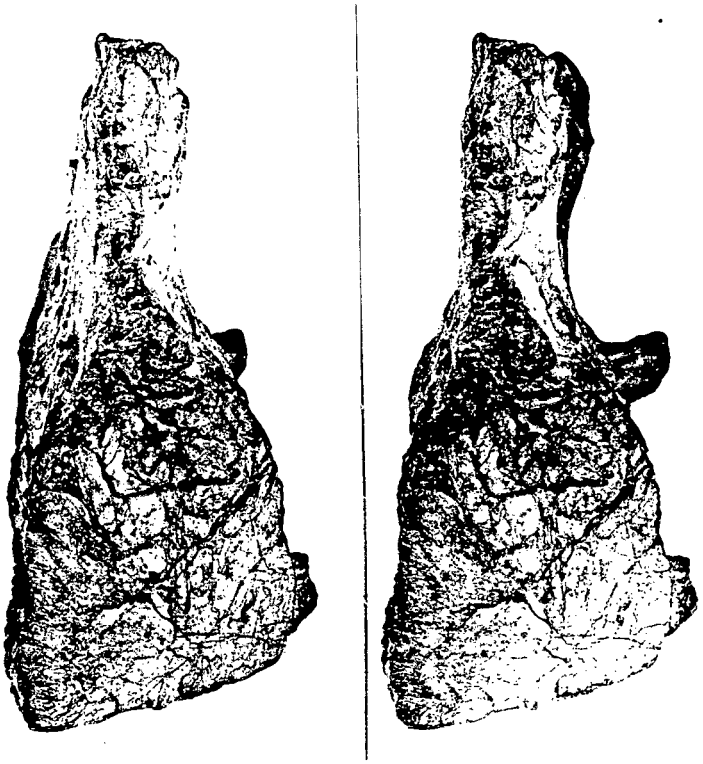

Fig. 61o Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Right lateral view of skull roof. Scale 20mm.

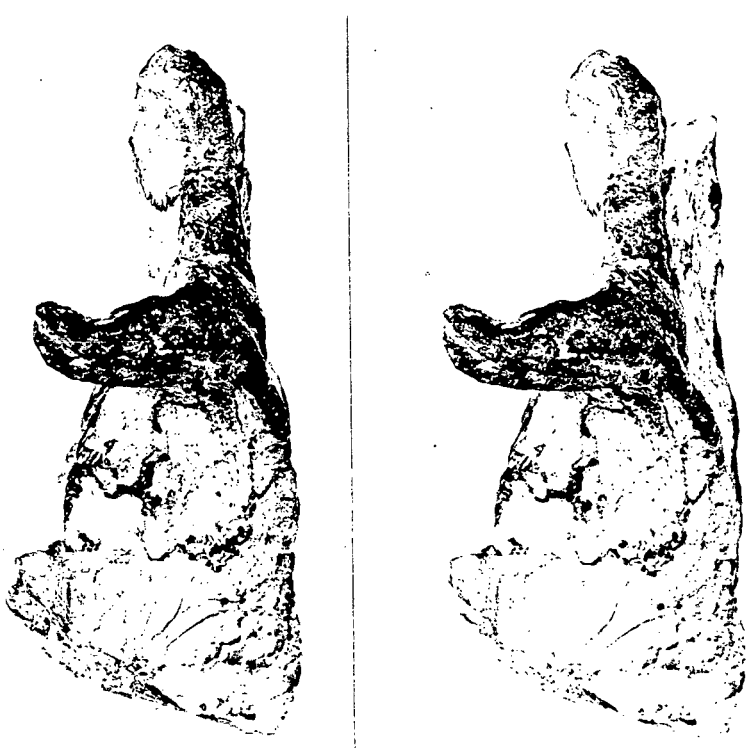

Fig. 61p Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Left lateral view of skull roof. Scale 20mm.

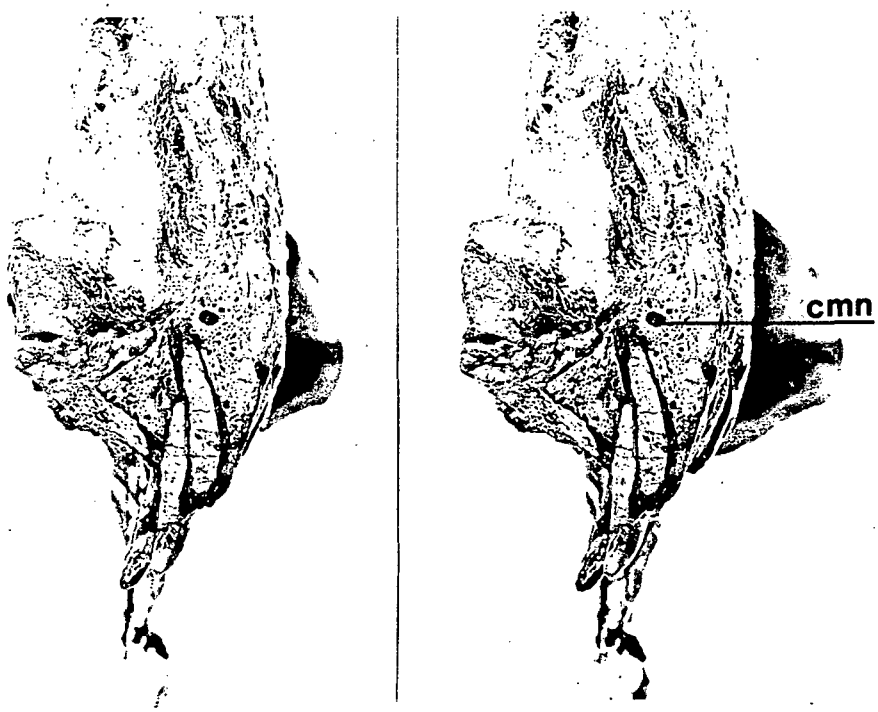

Fig. 61q Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Posterior view of section through right upper postcanine region. Scale 20mm.

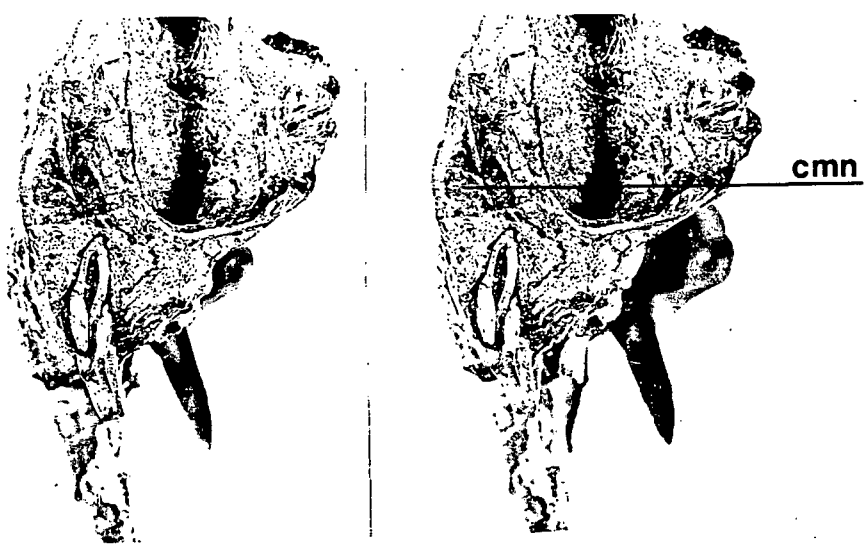

Fig. 61r Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Posterior view of section through left upper postcanine region. Scale 20mm.

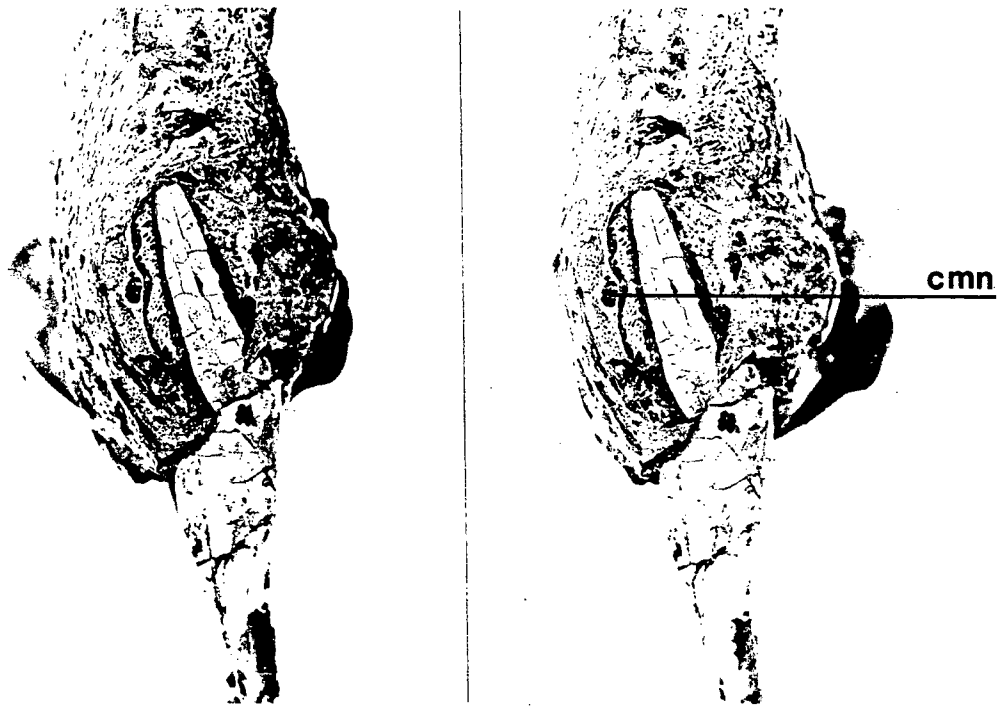

Fig. 61s Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Anterior view of section through hindmost incisor in right premaxilla. Scale 20mm.

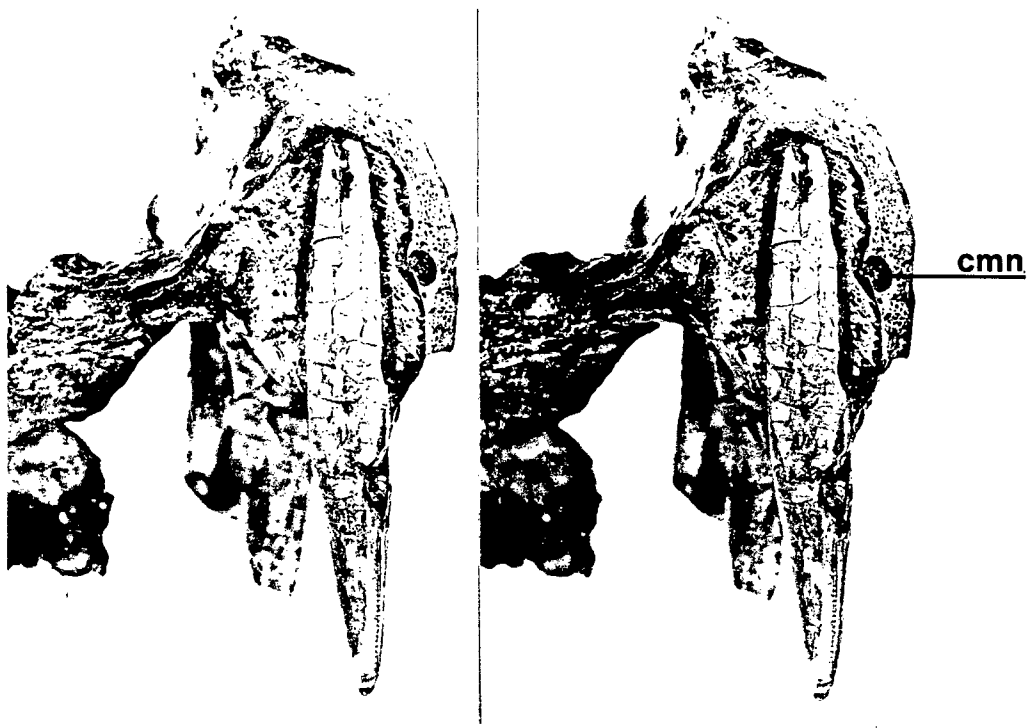

Fig. 61t Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Posterior view of section through hindmost incisor in right premaxilla. Scale 20mm.

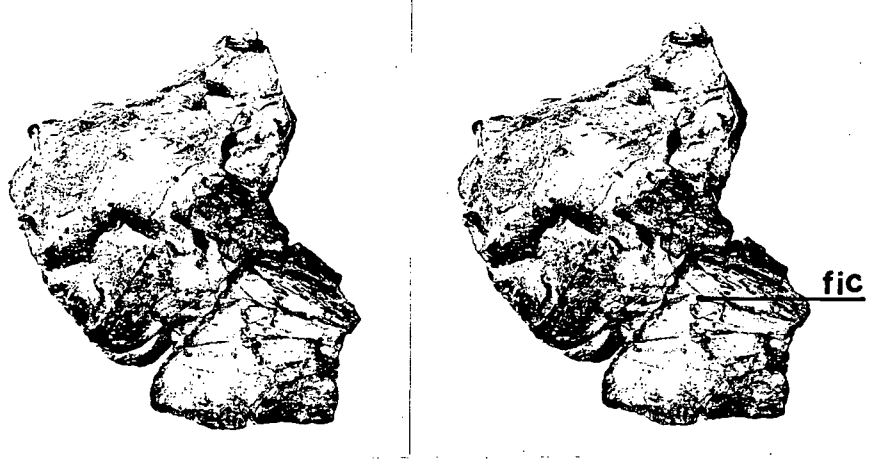

Fig. 61u Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Right lateral view of braincase. Scale 20mm.

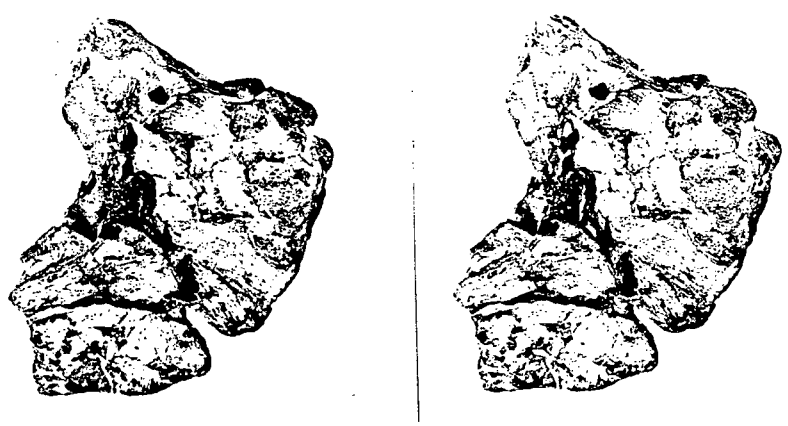

Fig. 61v Stereophotograph of the type of *Lycosuchus keyseri* GS C60. Left lateral view of braincase. Scale 20mm.

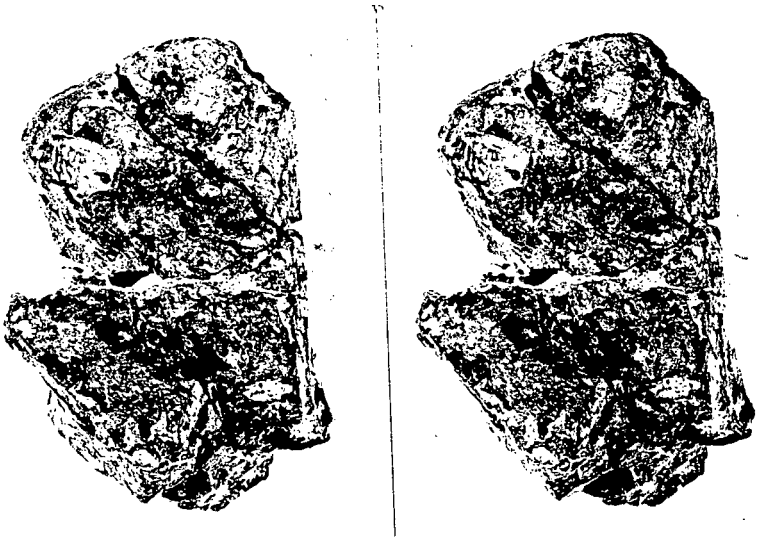

Fig. 62a Stereophotograph of the type skull of *Pardosuchus whaitsi* SAM 1077. Left lateral view. Scale 20mm.

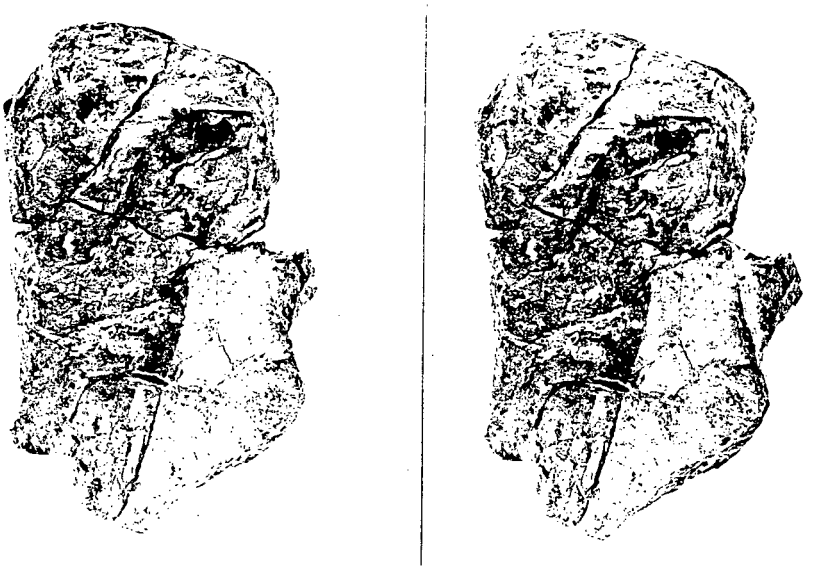

Fig. 62b Stereophotograph of the type skull of *Pardosuchus whaitsi* SAM 1077. Right lateral view. Scale 20mm.

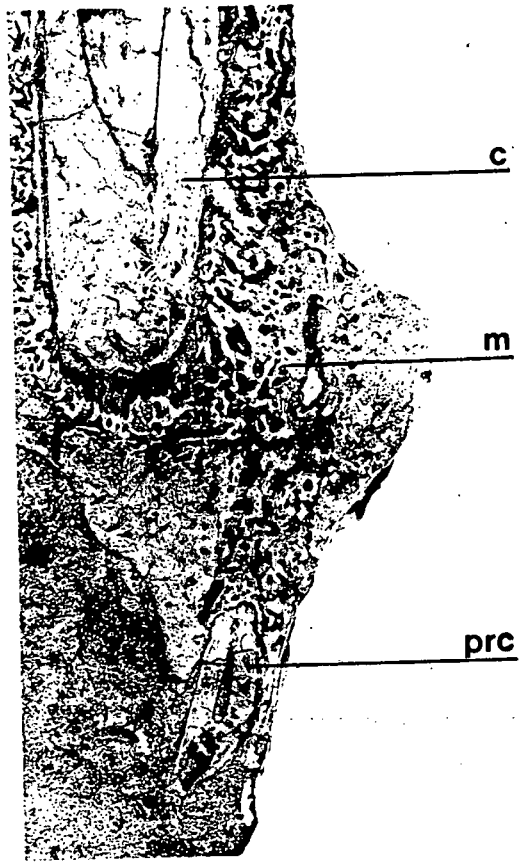

Fig. 62c Photograph of the type skull of *Pardosuchus whaitsi* SAM 1077 Oblique transverse section through canine region. Scale 20mm.

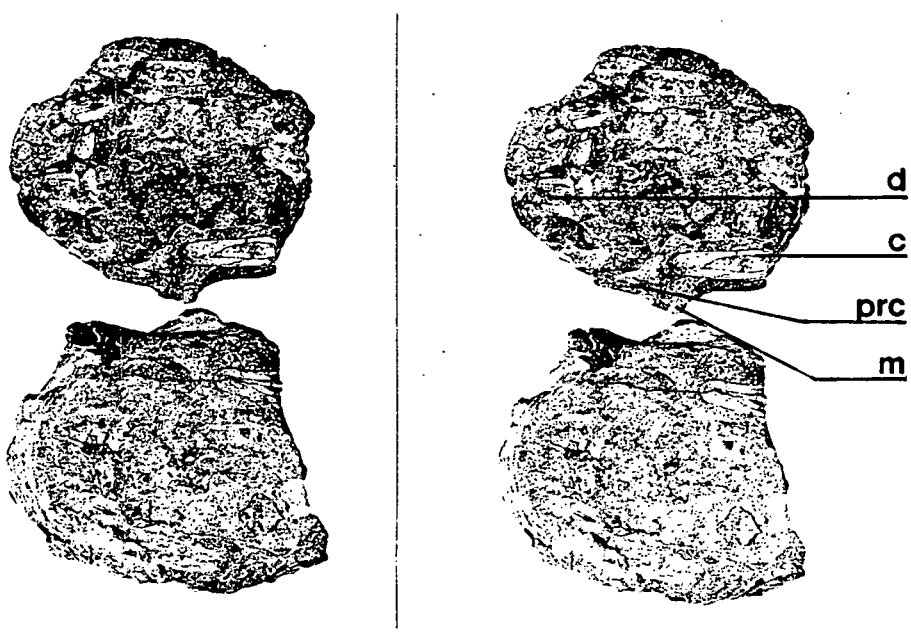

Fig. 62d Stereophotograph of the type skull of *Pardosuchus whaitsi* SAM 1077. Matching, oblique, transverse sections through the canine region. Scale 20mm.

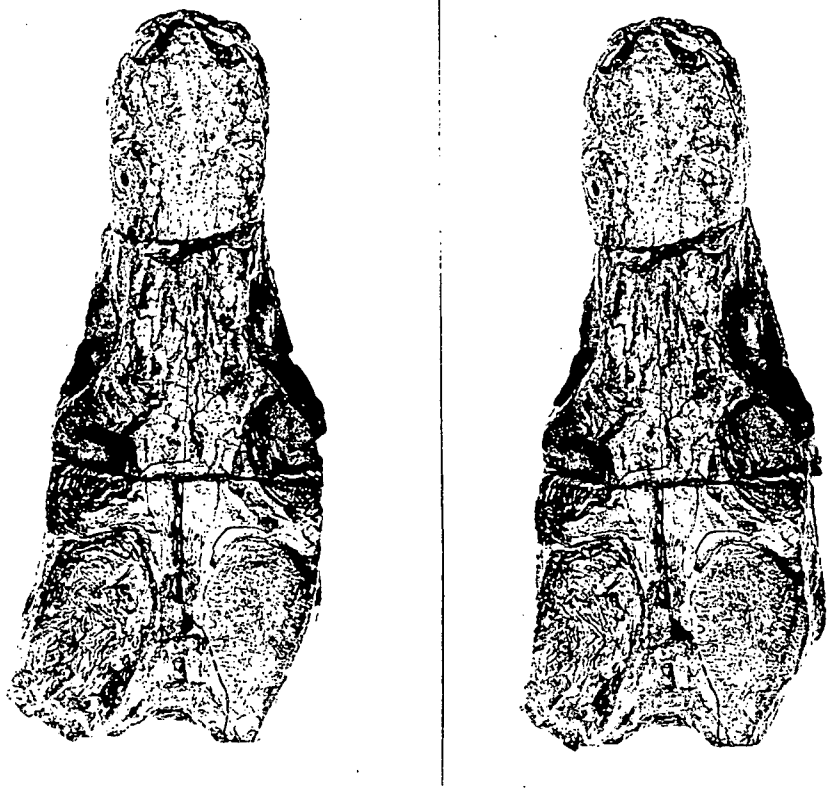

Fig. 63a Stereophotograph of the type skull of *Pristerognathoides minor* SAM 3415. Dorsal view. Scale 20mm.

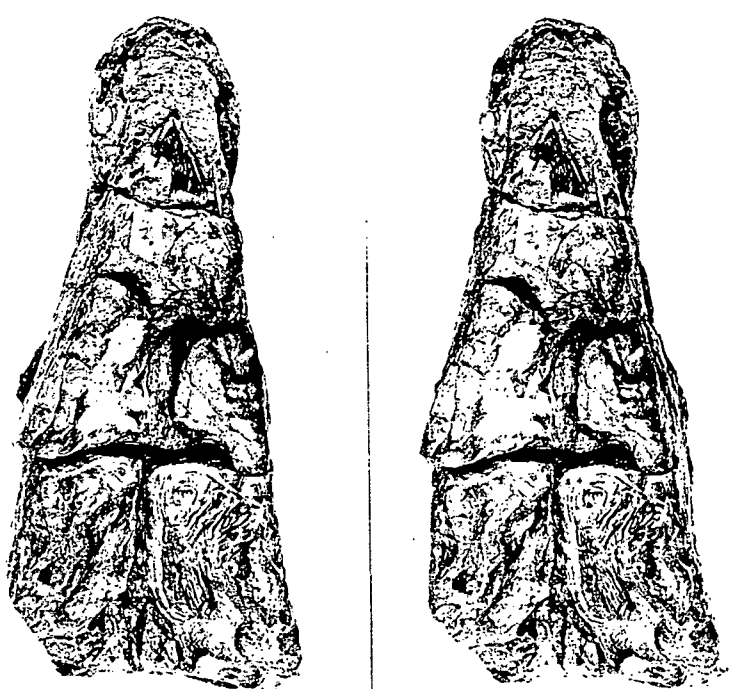

Fig. 63b Stereophotograph of the type skull of *Pristerognathoides minor* SAM 3415. Ventral view. Scale 20mm.

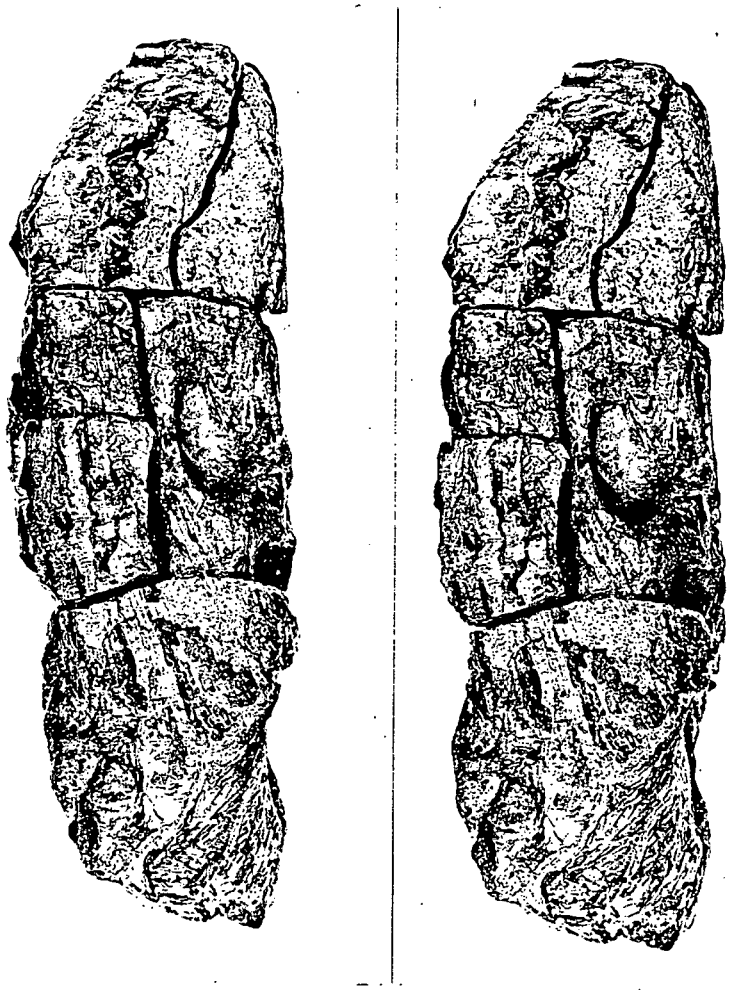

Fig. 63c Stereophotograph of the type skull of ***Pristerognathoides minor*** SAM 3415. Left lateral view. Scale 20mm.

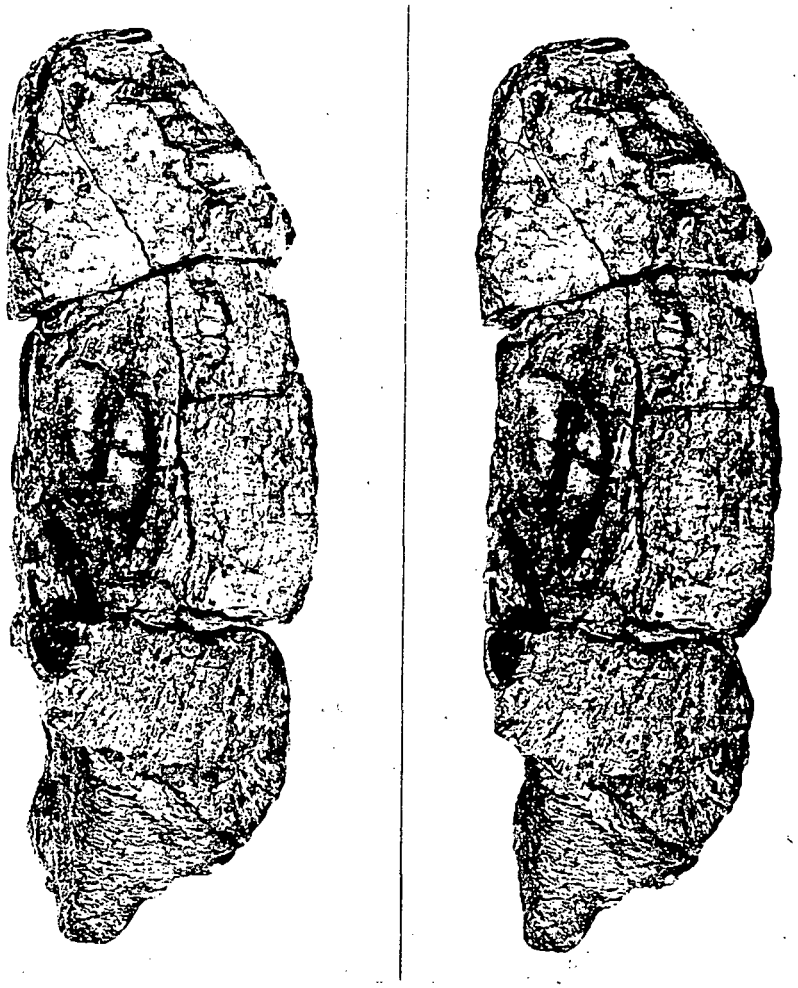

Fig. 63d Stereophotograph of the type skull of ***Pristerognathoides minor*** SAM 3415. Right lateral view. Scale 20mm.

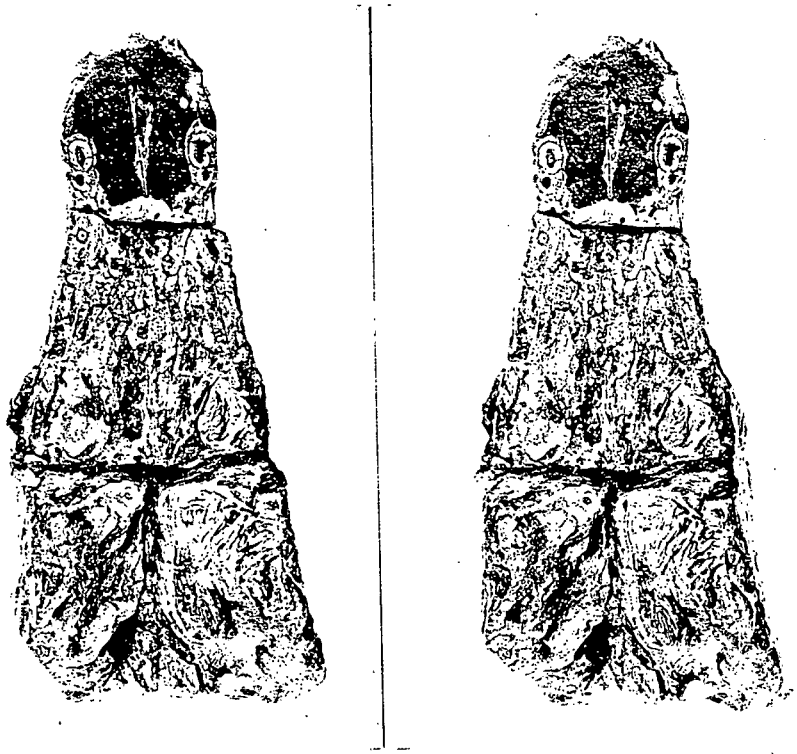

Fig. 63e Stereophotograph of the type skull of ***Pristerognathoides minor*** SAM 3415. Ventral view of palate. Scale 20mm.

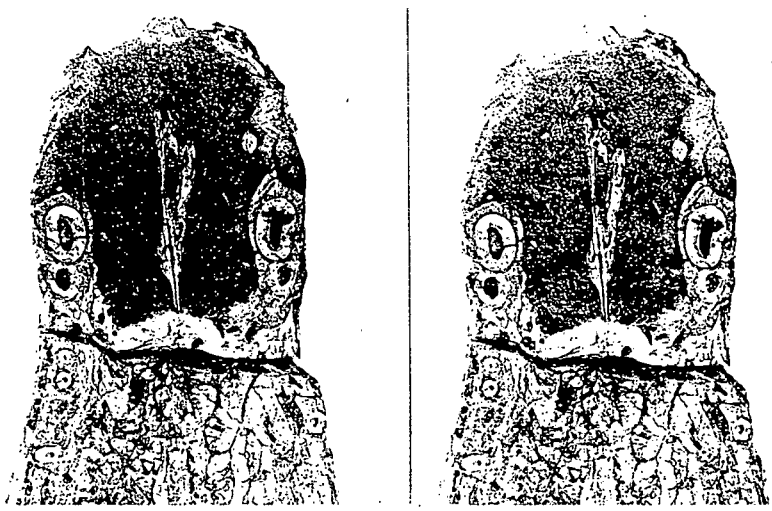

Fig. 63f Stereophotograph of the type skull of ***Pristerognathoides minor*** SAM 3415. Ventral close-up anterior palate. Scale 20mm.

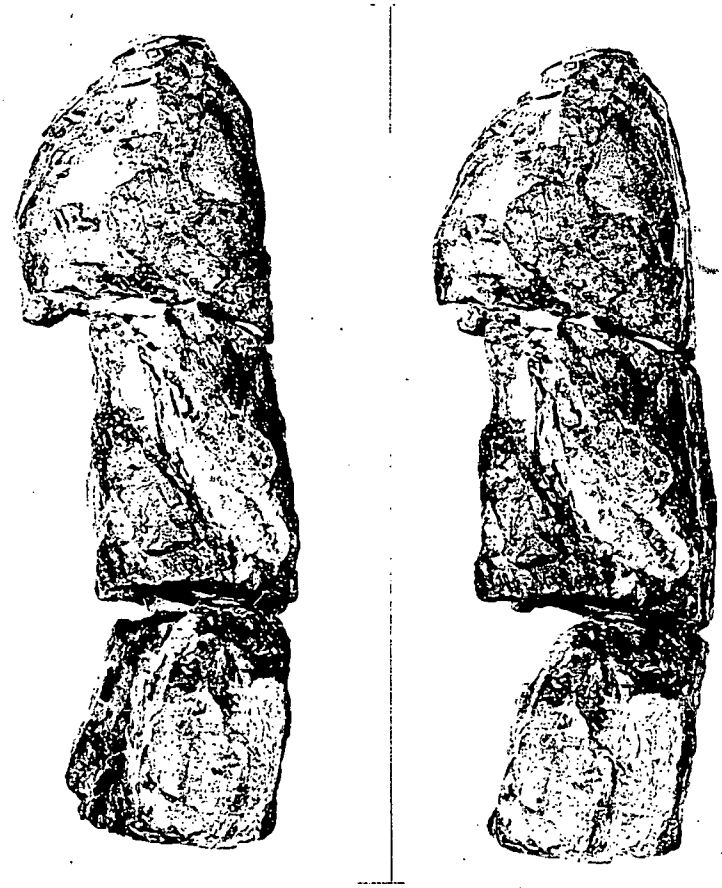

Fig. 64a Stereophotograph of the type skull of *Pristerognathoides parvus* SAM 3611. Left lateral view. Scale 20mm.

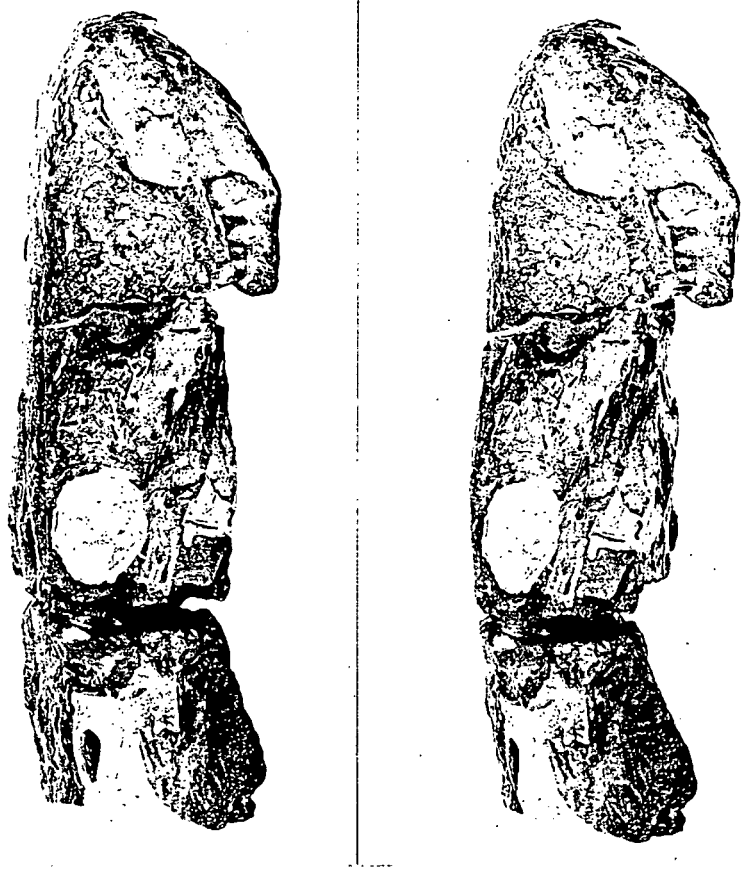

Fig. 64b Stereophotograph of the tyoe skull of *Pristerognathoides parvus* SAM 3611. Right lateral view. Scale 20mm.

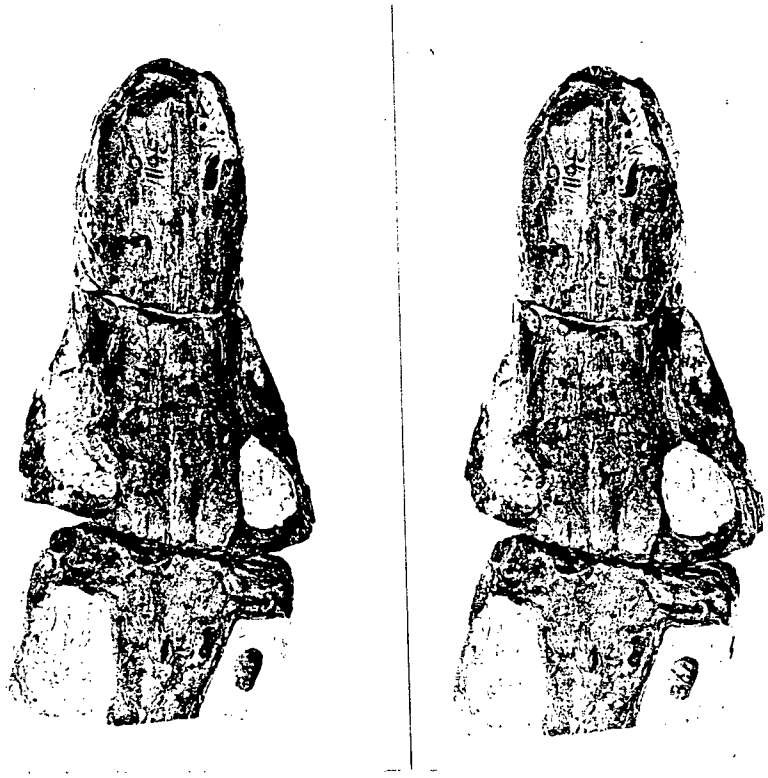

Fig. 64c Stereophotograph of the type skull of *Pristerognathoides parvus* SAM 3611. Dorsal view. Scale 20mm.

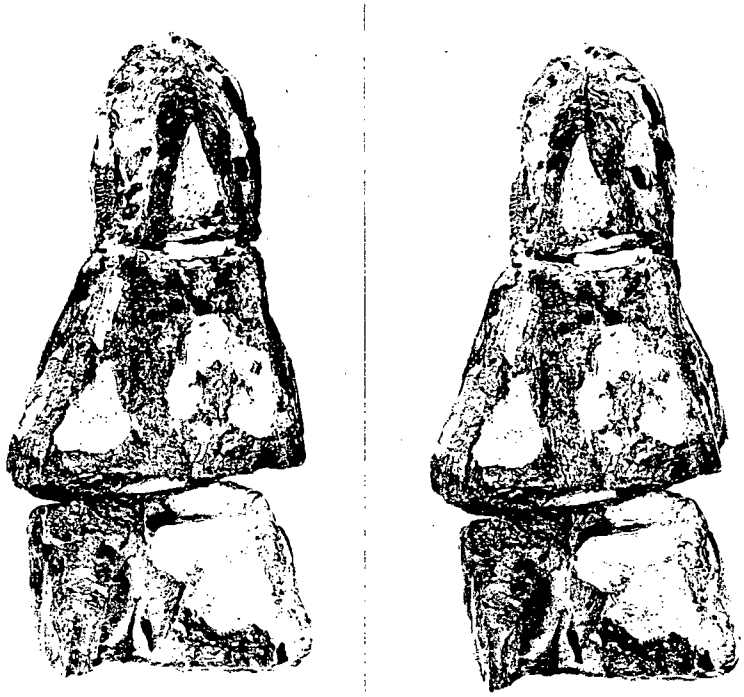

Fig.64d Stereophotograph of the type skull of *Pristerognathoides parvus* SAM 3611. Ventral view. Scale 20mm.

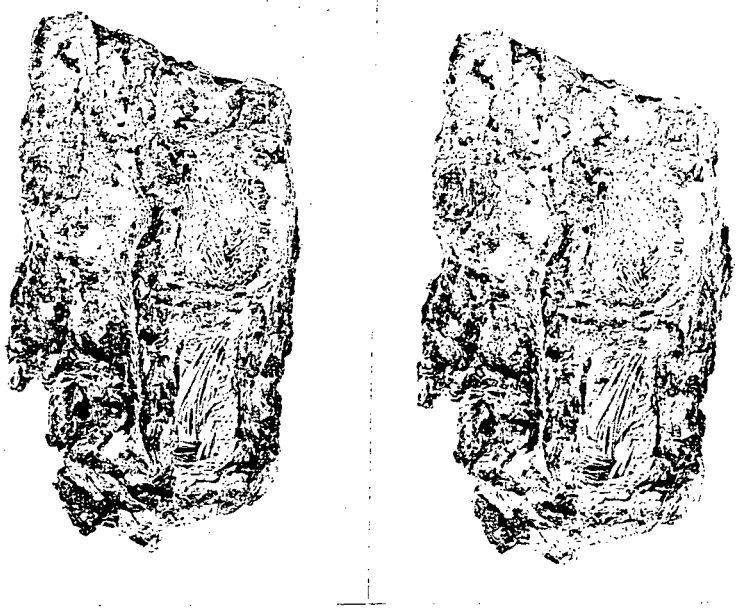

Fig. 65a Stereophotograph of the type skull of *Pristerognathoides (=Maraisaurus) parvus* SAM 11944. Left lateral view. Scale 20mm.

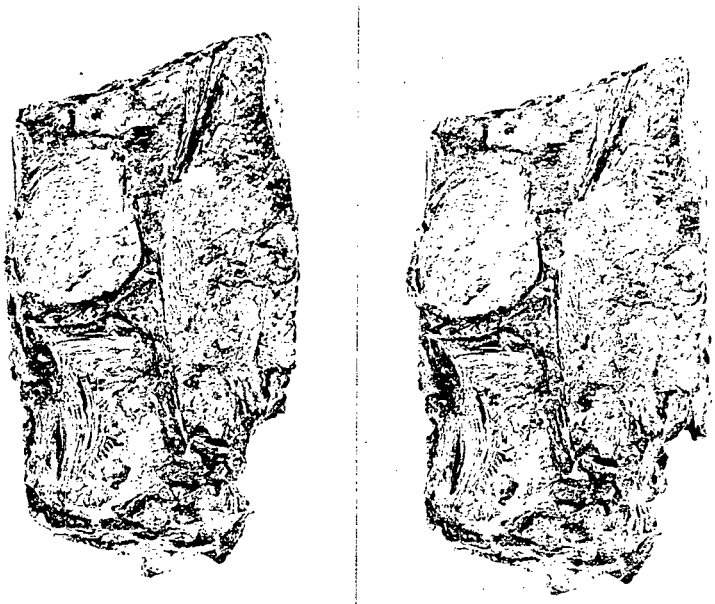

Fig. 65b Stereophotograph of the type skull of *Pristerognathoides (=Maraisaurus) parvus*. SAM 11944. Right lateral view. Scale 20mm.

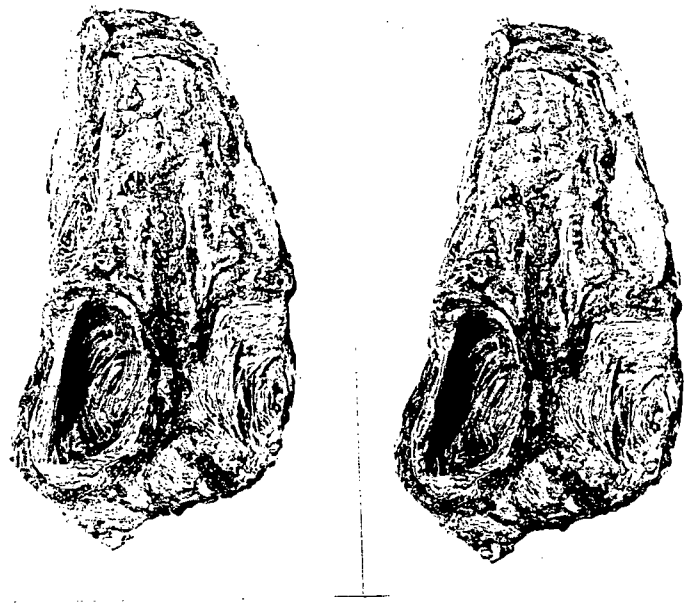

Fig. 65c Stereophotograph of the type skull of *Pristerognathoides (=Maraisaurus) parvus* SAM 11944. Dorsal view. Scale 20mm.

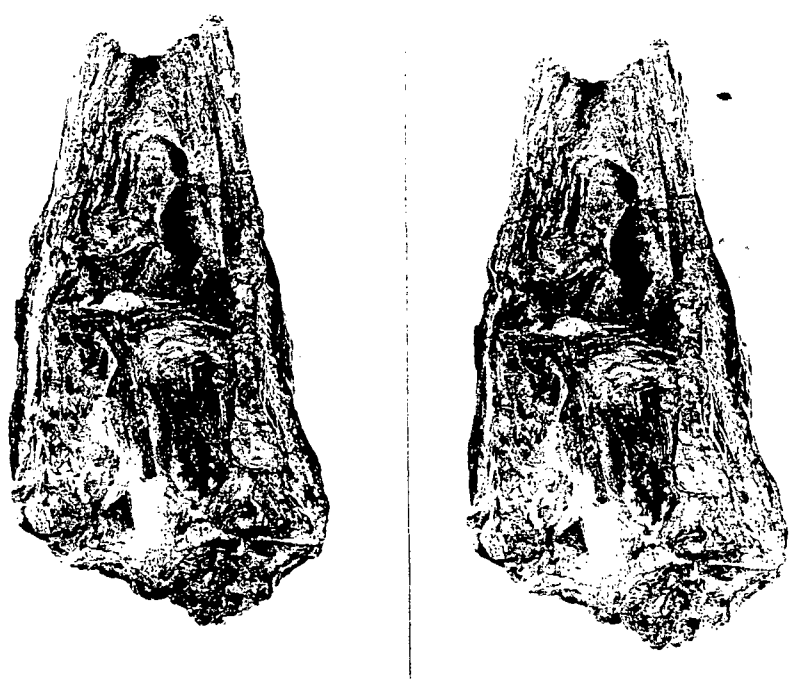

Fig. 65d Stereophotograph of the type skull of *Pristerognathoides (=Maraisaurus) parvus* SAM 11944. Ventral view. Scale 20mm.

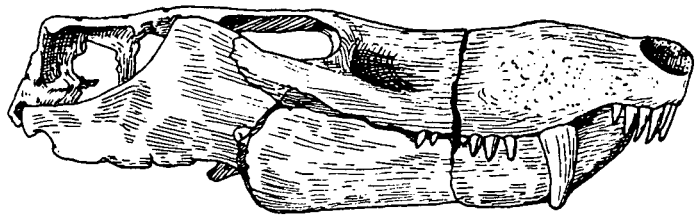

Fig. 66a Right lateral view of the type of *Pristerognathoides peyeri* UM 1936 II 9. From Broili and Schröder (1936b). Scale 20mm.

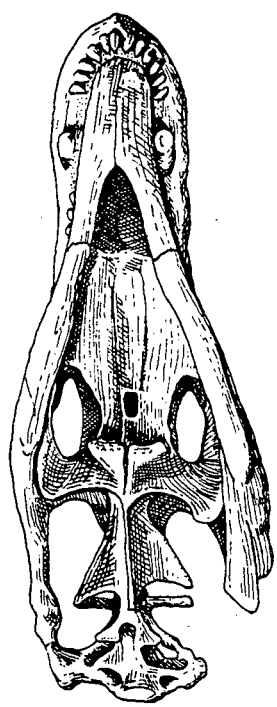

Fig. 66b Ventral view of the type of *Pristerognathoides peyeri* UM 1936 II 9. From Broili and Schröder (1936b). Scale 20mm.

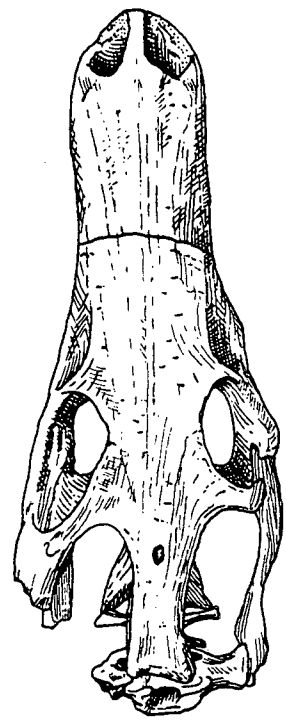

Fig. 66c Dorsal view of the type of *Pristerognathoides peyeri* UM 1936 II 9. From Broili and Schröder (1936b). Scale 20mm.

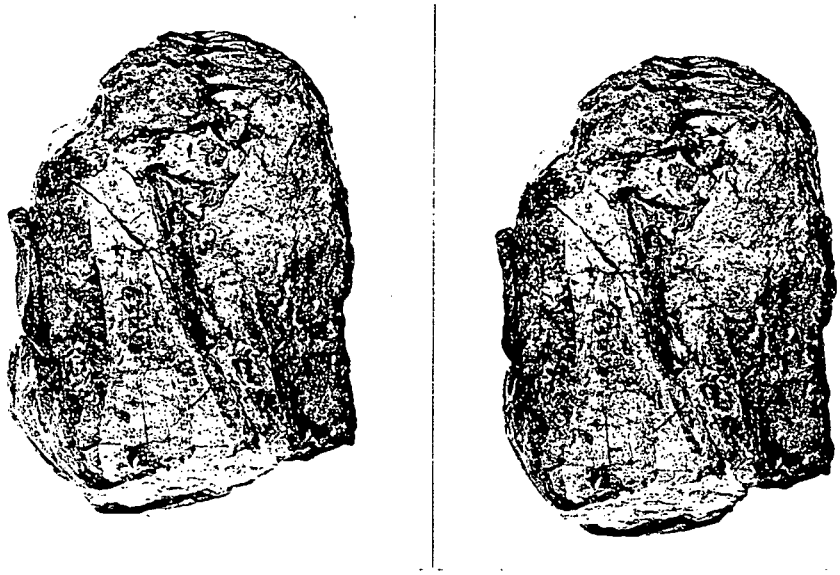

Fig 67a Stereophotograph of the type of *Pristerognathoides roggeveldensis* SAM 9356a. Left lateral view. Scale 20mm.

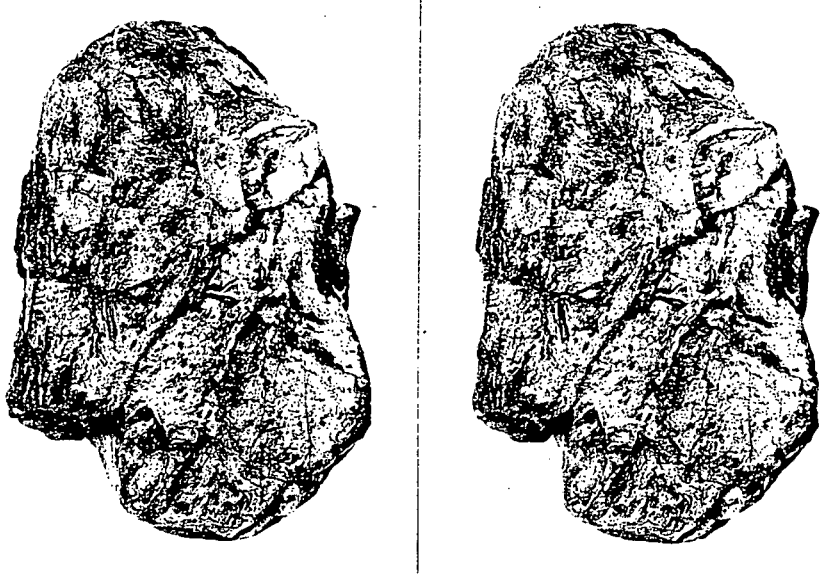

Fig. 67b Stereophotograph of the type of *Pristerognathoides roggeveldensis* SAM 9356a. Right lateral view. Scale 20mm.

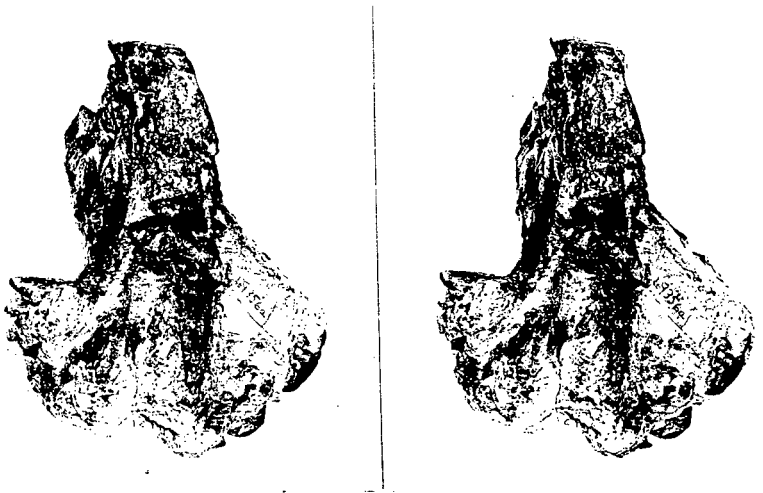

Fig. 67c Stereophotograph of the type of ***Pristerognathoides roggeveldensis*** SAM 9356a. Dorsolateral view of posterior portion of skull. Scale 20mm.

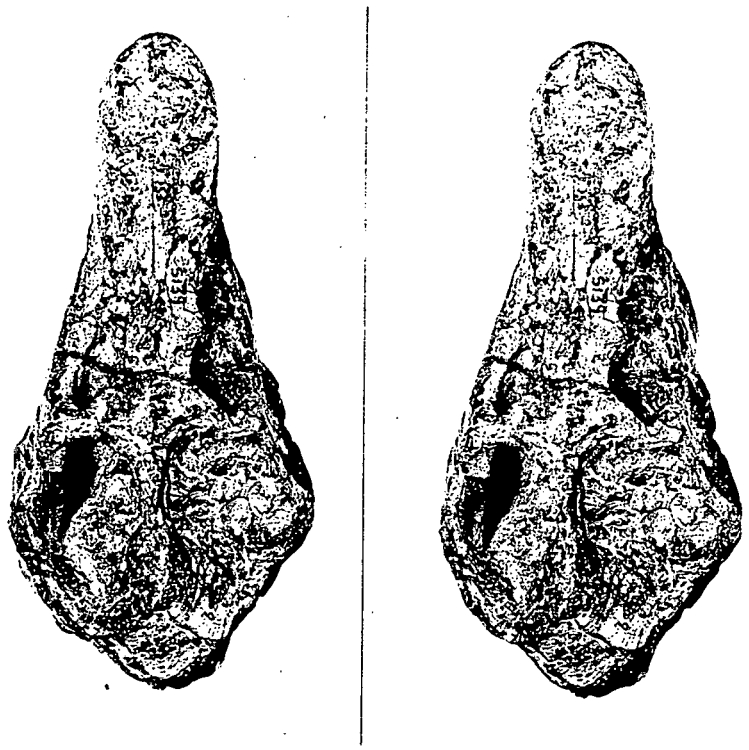

Fig. 68a Stereophotograph of the type skull of ***Pristerognathoides vanderbyli*** MM 5139. Dorsal view. Scale 20mm.

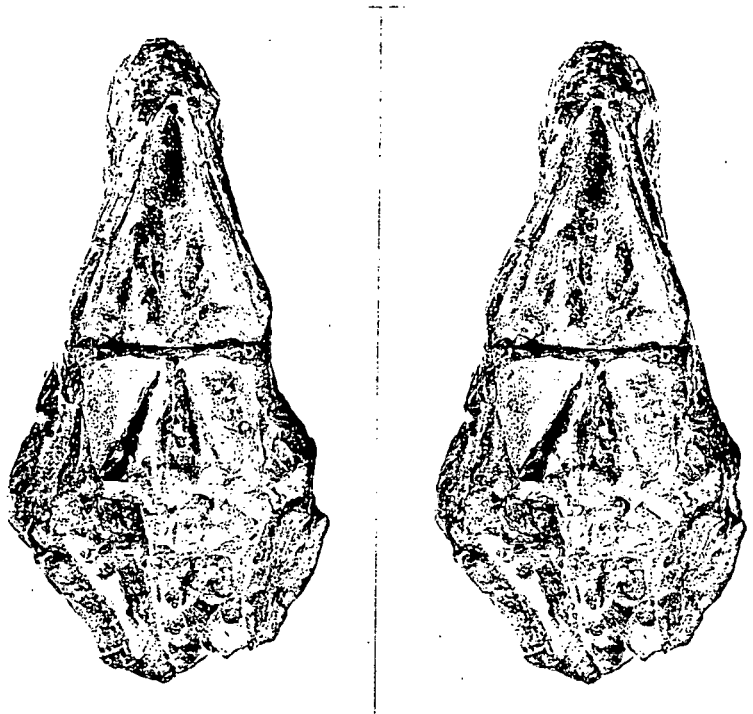

Fig. 68b Stereophotograph of the type skull of ***Pristerognathoides vanderbyli*** MM 5139. Ventral view. Scale 20mm.

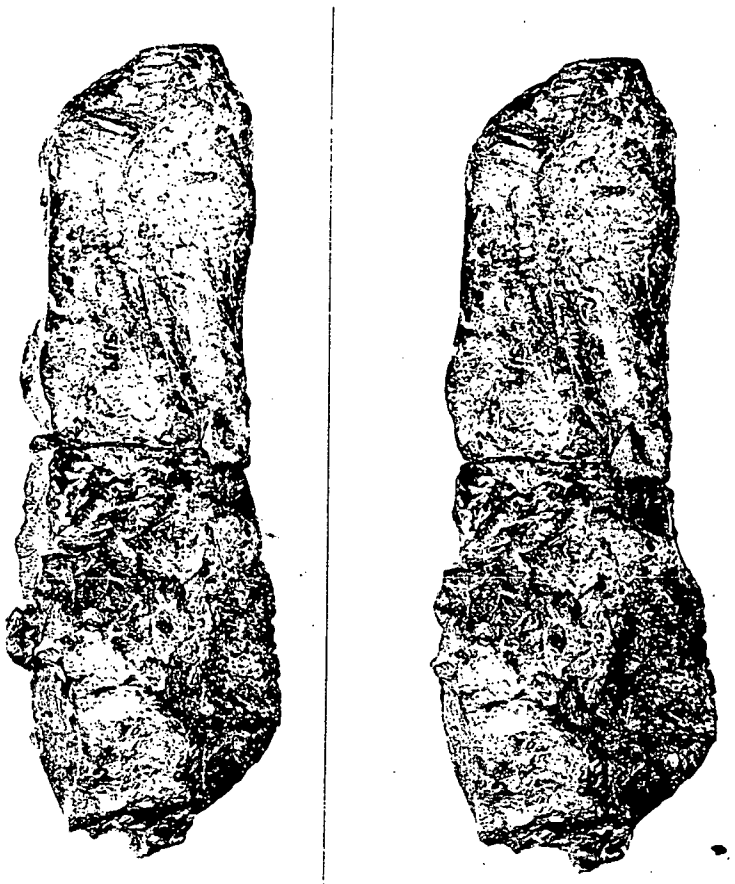

Fig. 68c Stereophotograph of the type skull of *Pristerognathoides vanderbyli* MM 5139. Left lateral view. Scale 20mm.

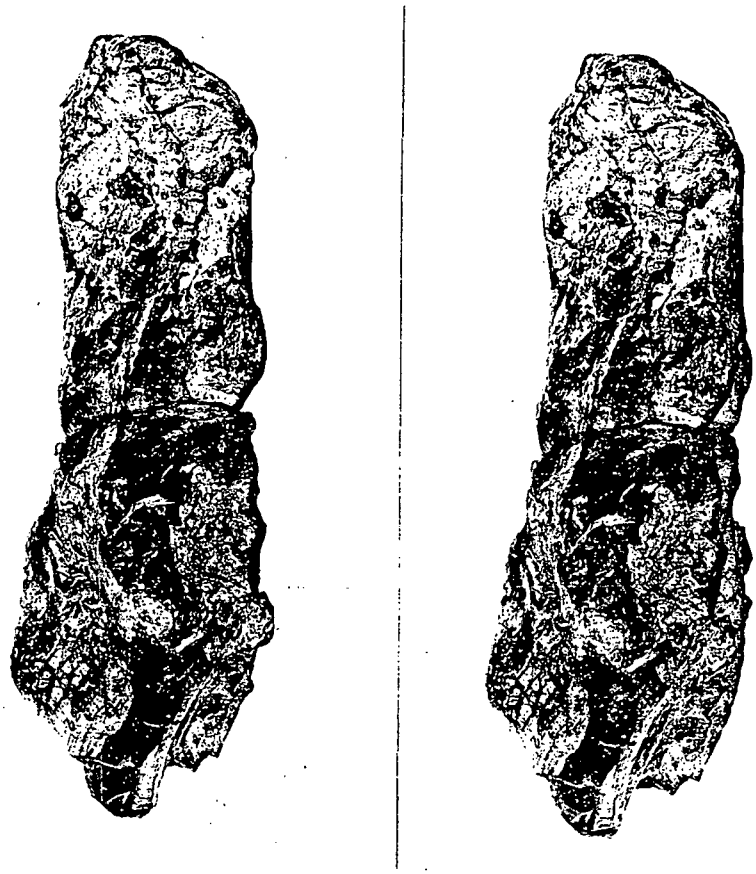

Fig. 68d Stereophotograph of the type skull of *Pristerognathoides vanderbyli* MM 5139. Right lateral view. Scale 20mm.

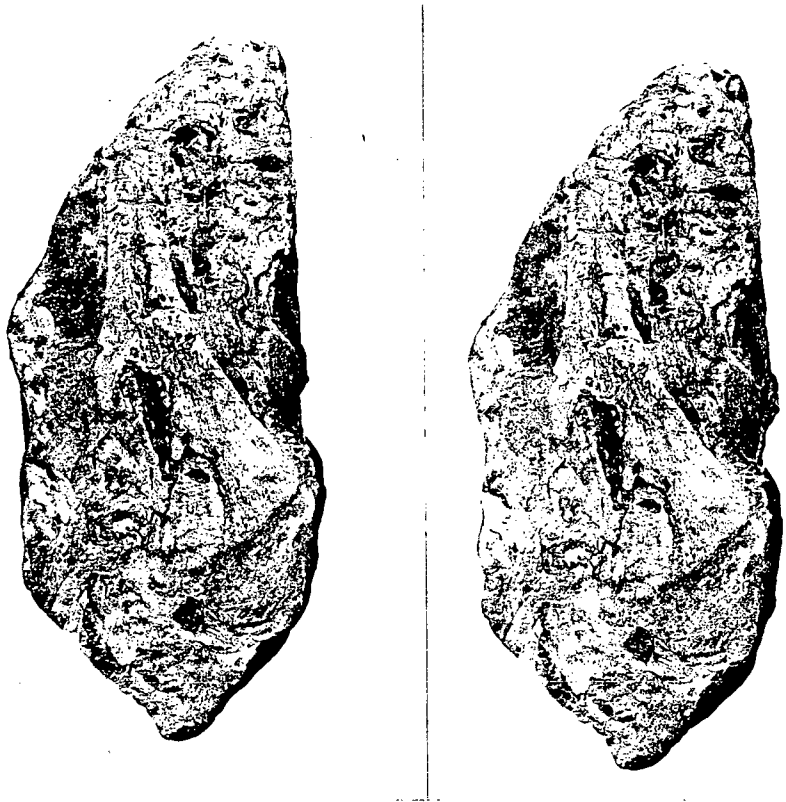

Fig. 69a Stereophotograph of the type skull of *Pristerognathoides vanwyki* SAM 6533. Left lateral view. Scale 20mm.

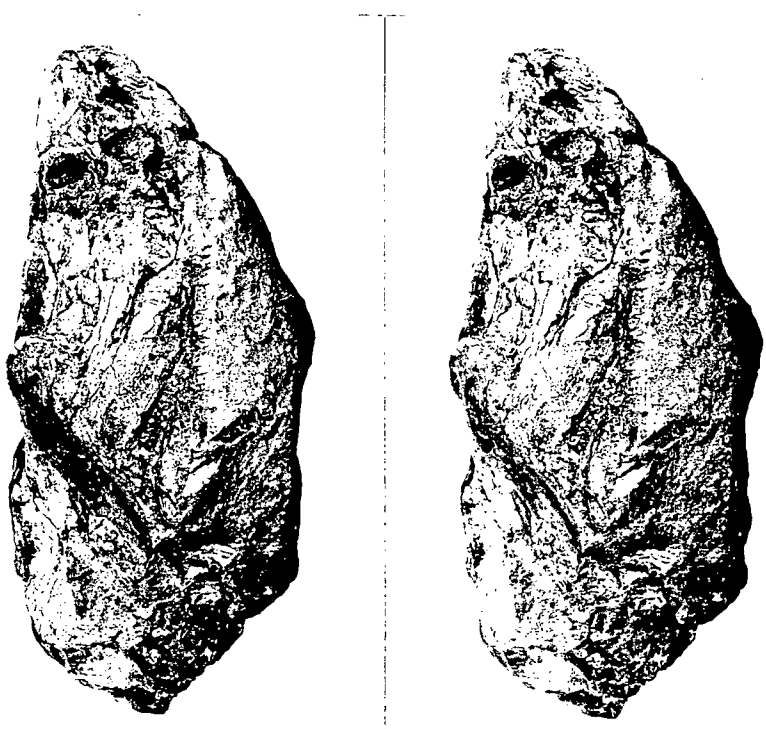

Fig. 69b Stereophotograph of the type skull of *Pristerognathoides vanwyki* SAM 6533. Right lateral view. Scale 20mm.

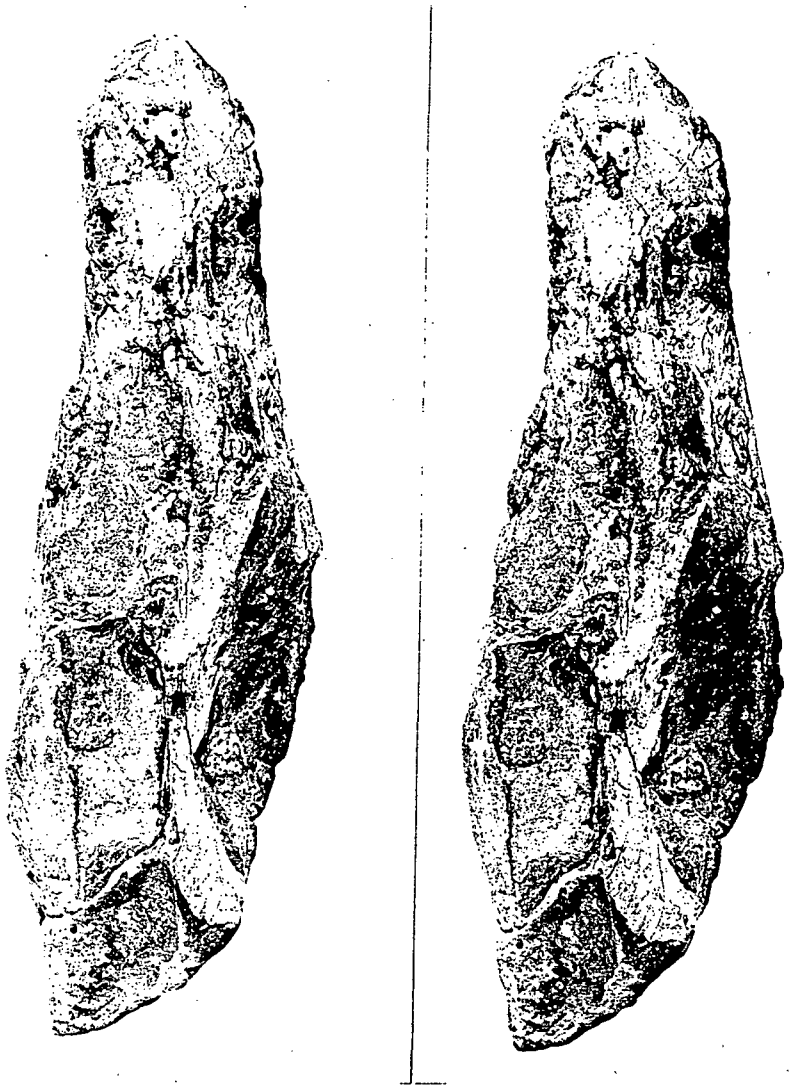

Fig. 69c Stereophotograph of the type skull of ***Pristerognathoides vanwyki*** SAM 6533. Dorsal view. Scale 20mm.

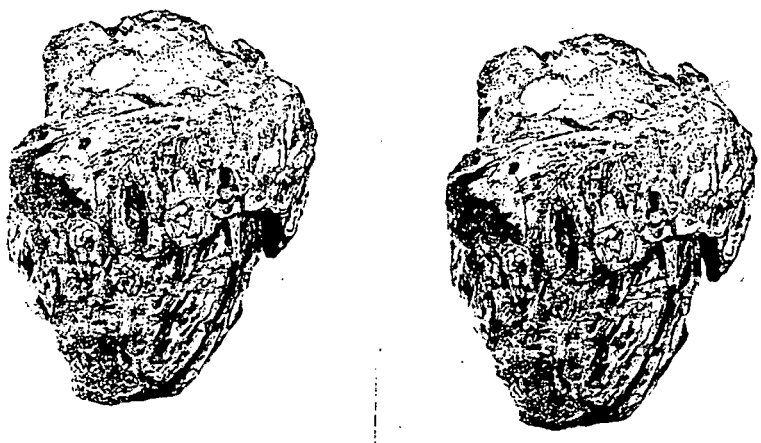

Fig. 70a Stereophotograph of the type of *Pristerognathus baini* SAM 583. Right lateral view. Scale 20mm.

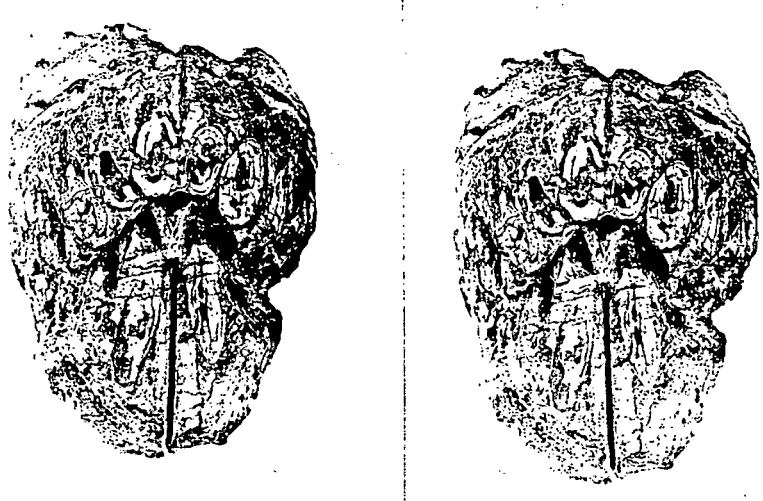

Fig. 70b Stereophotograph of the type of *Pristerognathus baini* SAM 583. Anterior view. Scale 20mm.

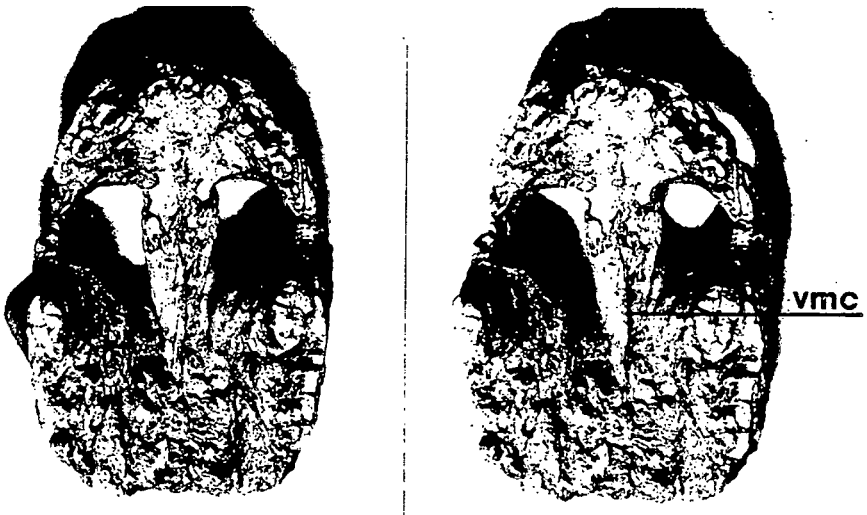

Fig. 71a Stereophotograph of the type of ***Pristerognathus polyodon*** BMNH R2581. Ventral view. Scale 20mm.

Fig. 71b Stereophotograph of the type of ***Pristerognathus polyodon*** BMNH R2581. Dorsal view. Scale 20mm.

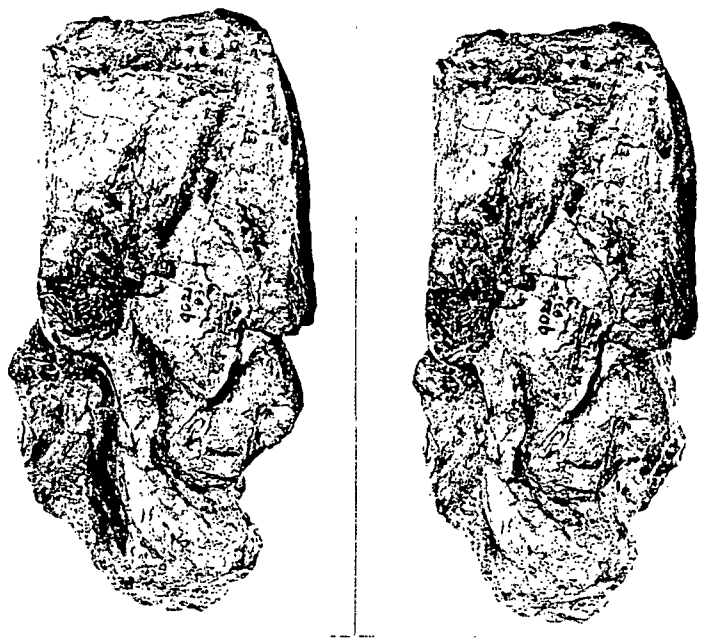

Fig. 72a Stereophotograph of the type skull of *Pristerosaurus microdon* SAM 9083. Right lateral view. Scale 20mm.

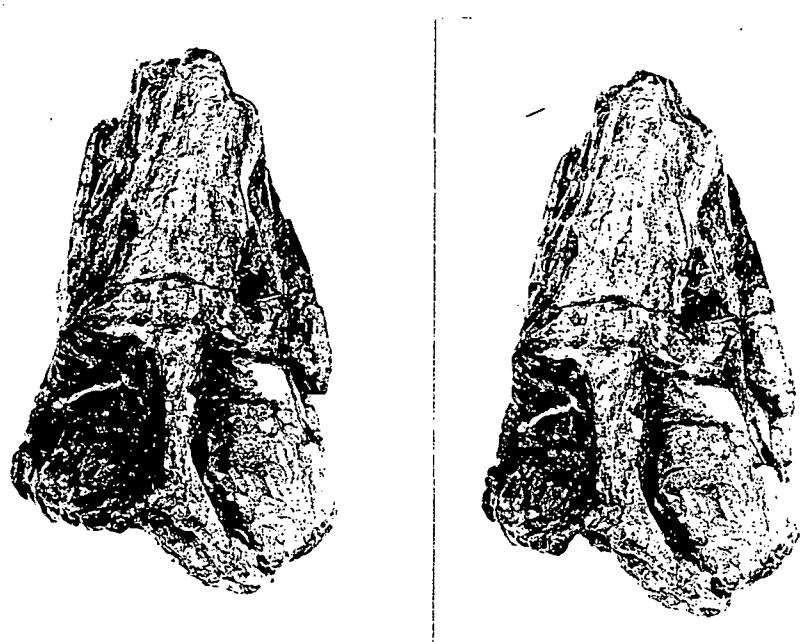

Fig. 72b Stereophotograph of the type skull of *Pristerosaurus microdon* SAM 9083. Dorsal view. Scale 20mm.

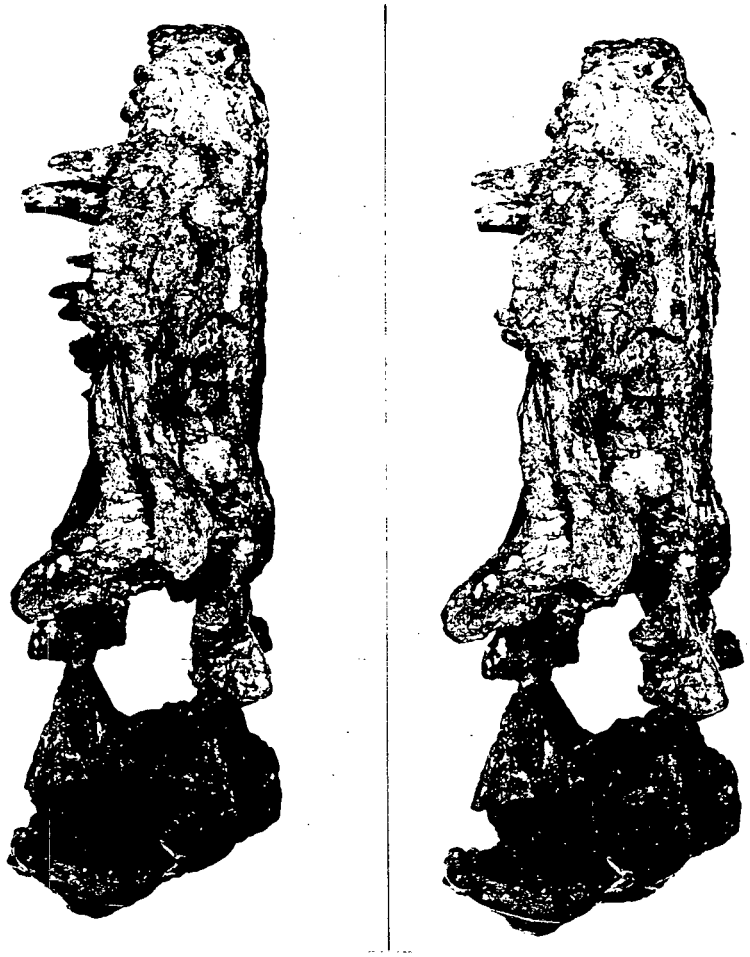

Fig. 73a Stereophotograph of the type skull of ***Ptomalestes avidus*** SAM 11942. Left lateral view. Scale 20mm.

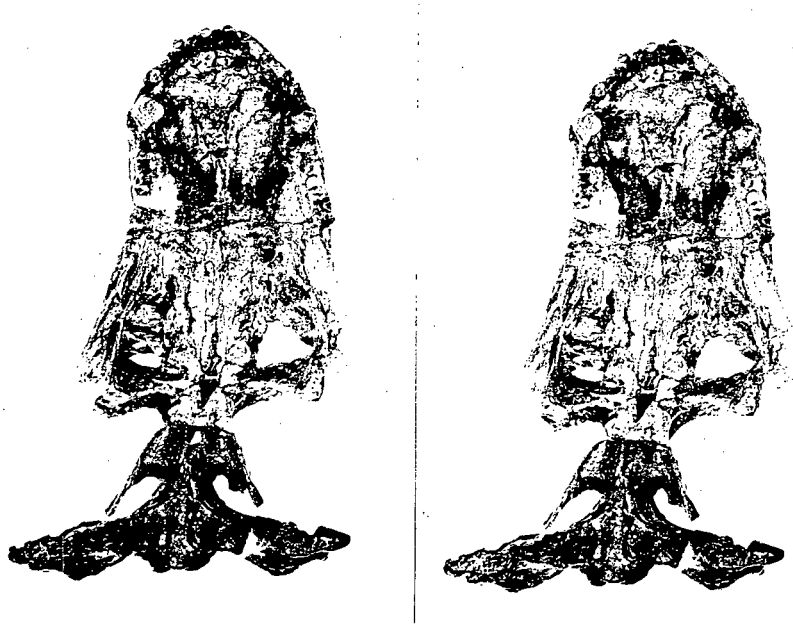

Fig. 73b Stereophotograph of the type skull of ***Ptomalestes avidus*** SAM 11942. Ventral view. Scale 20mm.

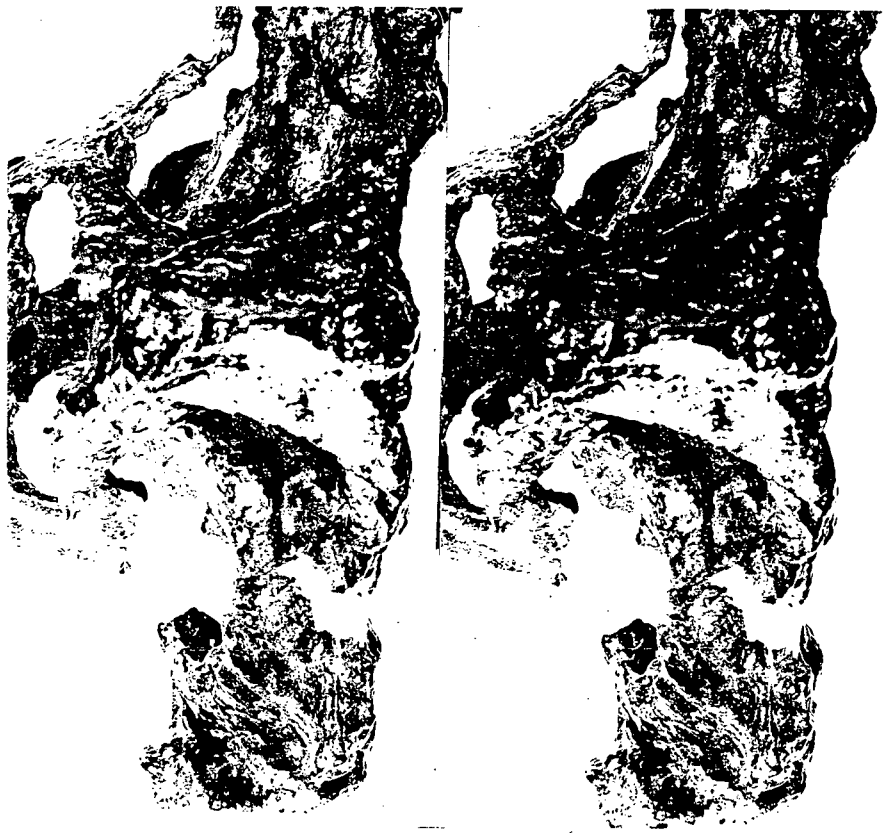

Fig. 73c Stereophotograph of the type skull of *Ptomalestes avidus* SAM 11942. Dorsal view of parietal region. Scale 20mm.

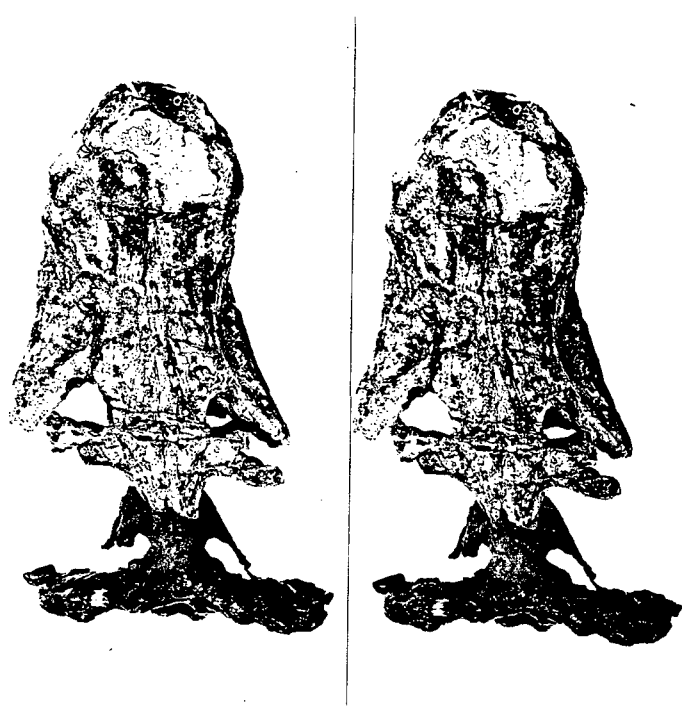

Fig 73d Stereophotograph of the type skull of *Ptomalestes avidus* SAM 11942. Dorsal view. Scale 20mm.

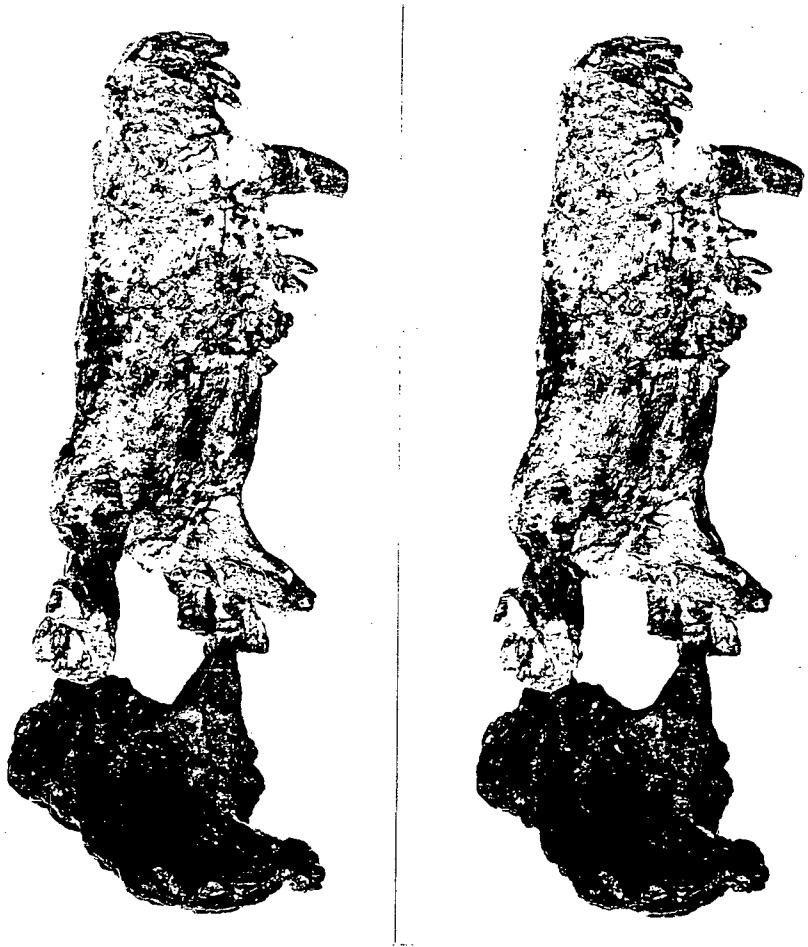

Fig 73e Stereophotograph of the type skull of *Ptomalestes avidus* SAM 11942. Right lateral view. Scale 20mm.

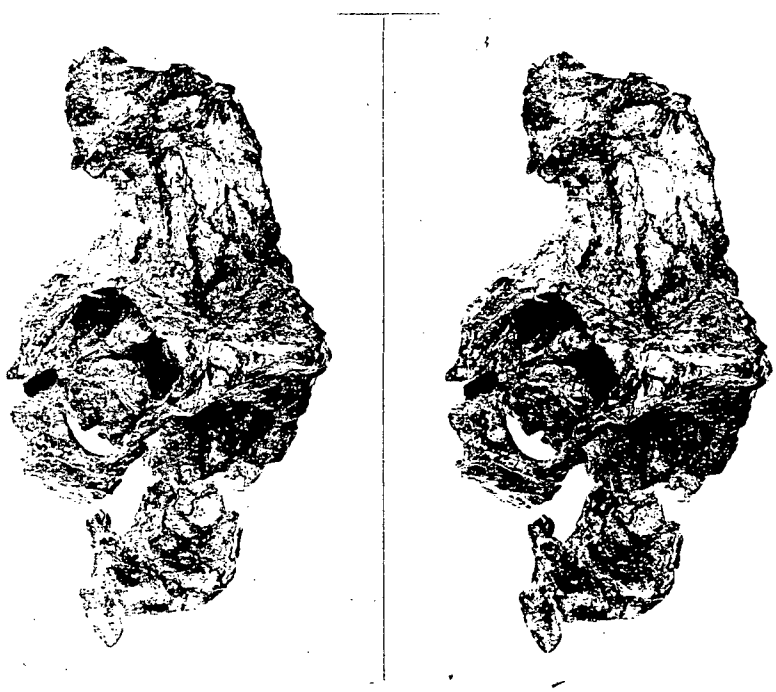

Fig 73f Stereophotograph of the type skull of *Ptomalestes avidus* SAM 11942. Anterior view of braincase and occiput. Scale 20mm.

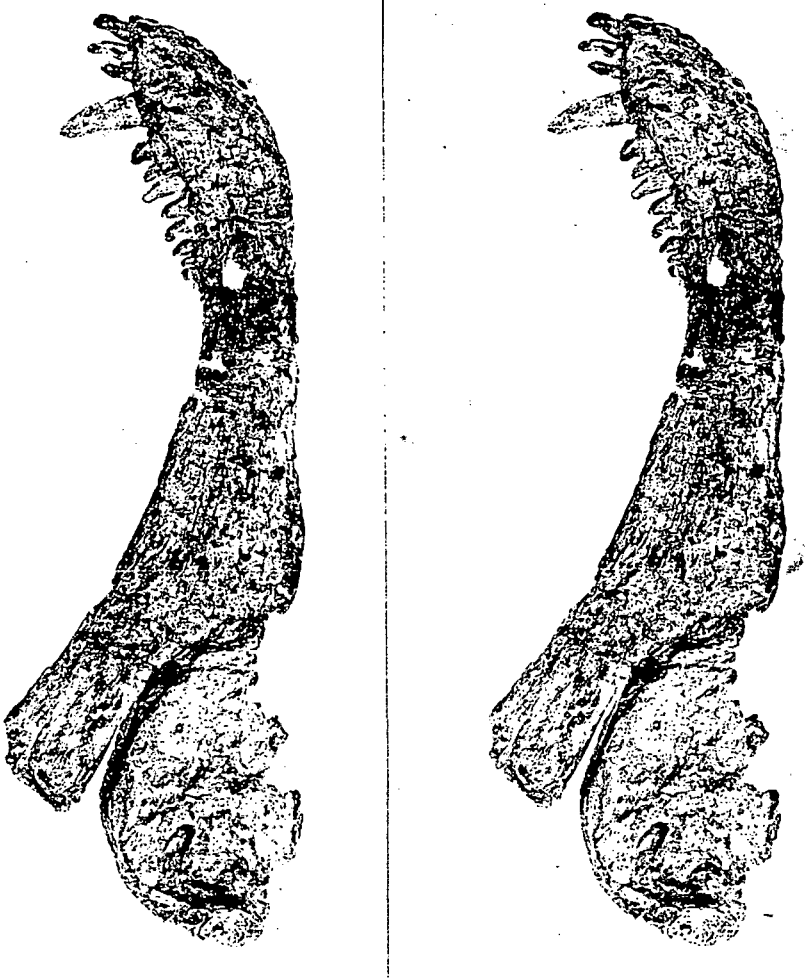

Fig. 73g Stereophotograph of the right jaw ramus of the type of *Ptomalestes avidus* SAM 11942. Lateral view. Scale 20mm.

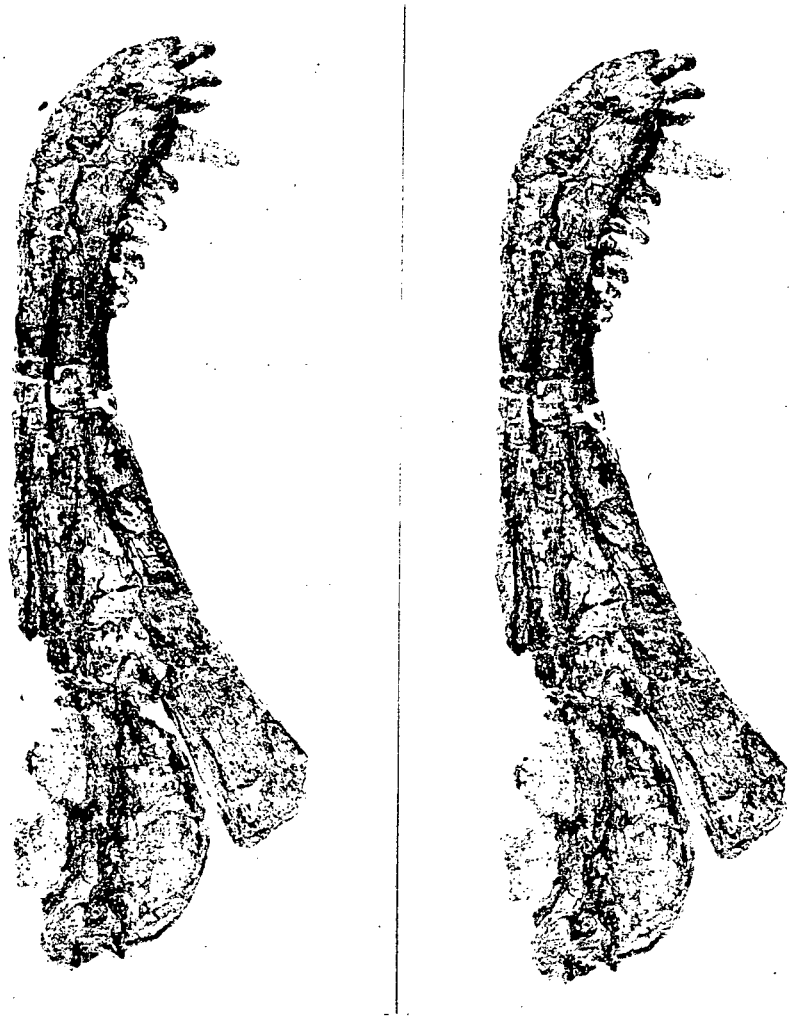

Fig. 73h Stereophotograph of the right jaw ramus of the type of *Ptomalestes avidus* SAM 11942. Medial view. Scale 20mm.

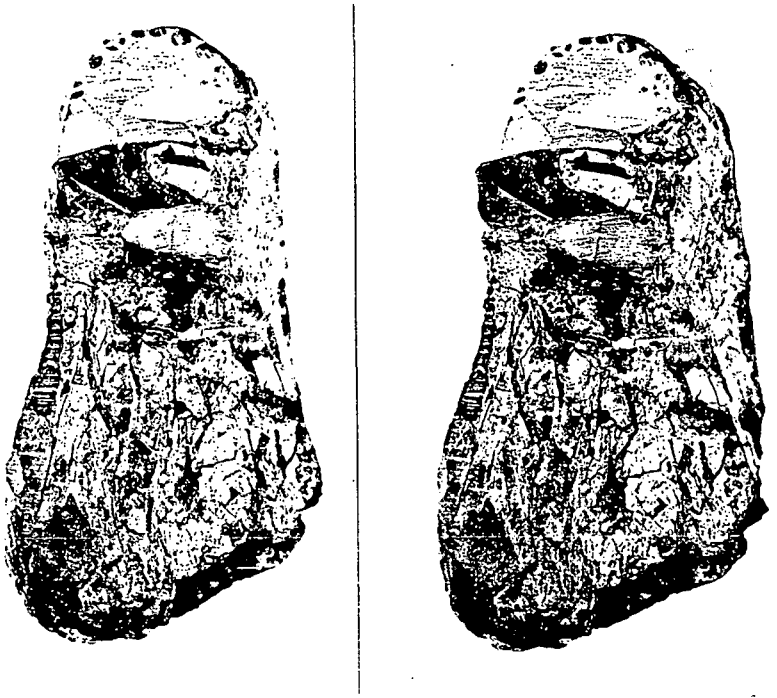

Fig. 74 Stereophotograph of the type of *Scylacoides ferox* AMNH 5558.
Ventral view. Scale 20mm.

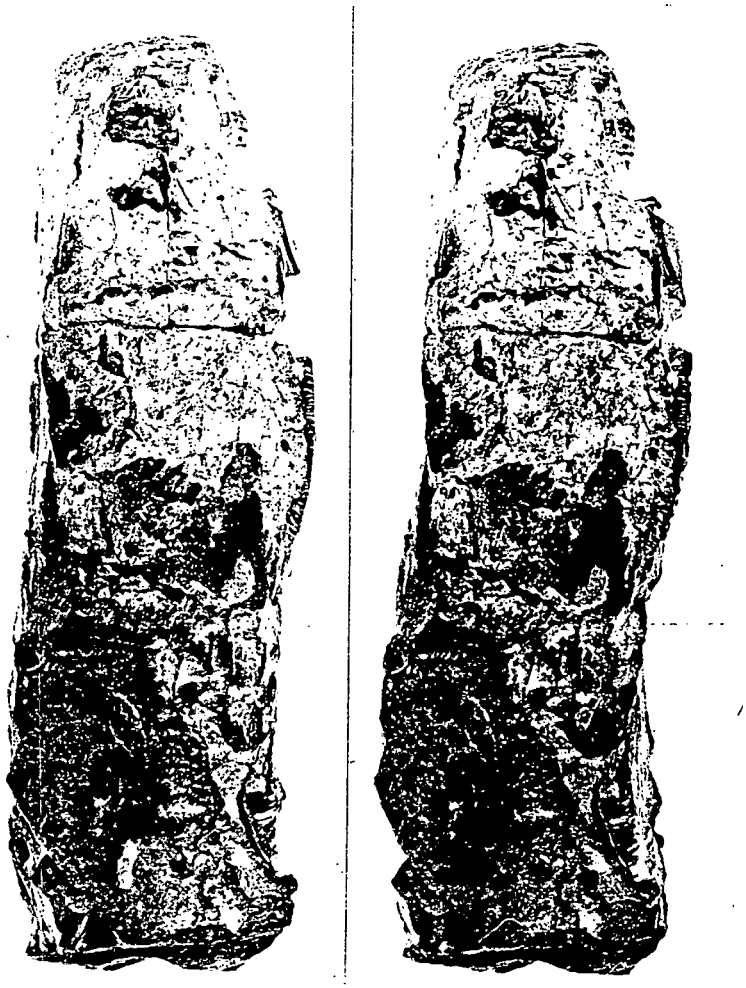

Fig. 75a Stereophotograph of the type skull of *Scylacosaurus sclateri* SAM 634. Right lateral view. Scale 20mm.

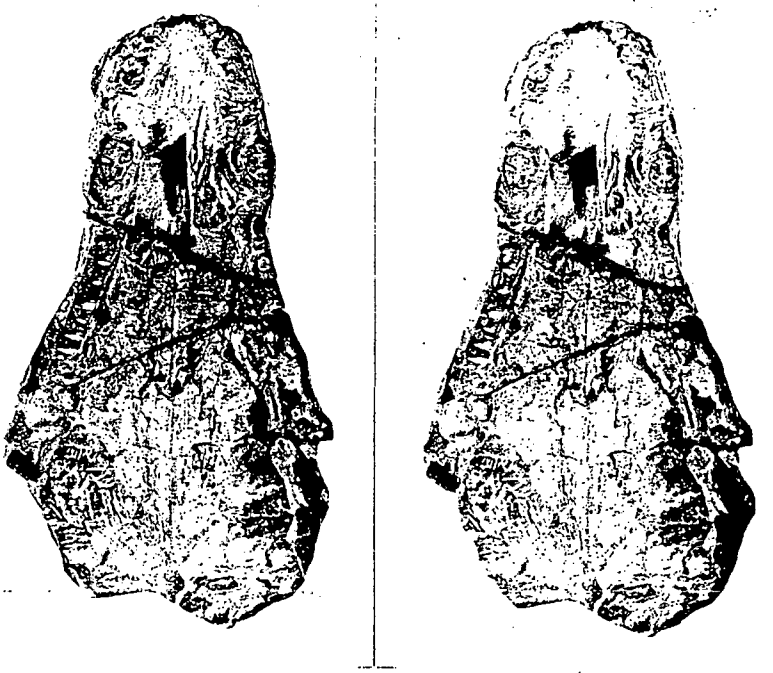

Fig. 75b Stereophotograph of the type skull of *Scylacosaurus sclateri* SAM 634. Ventral view. Scale 20mm.

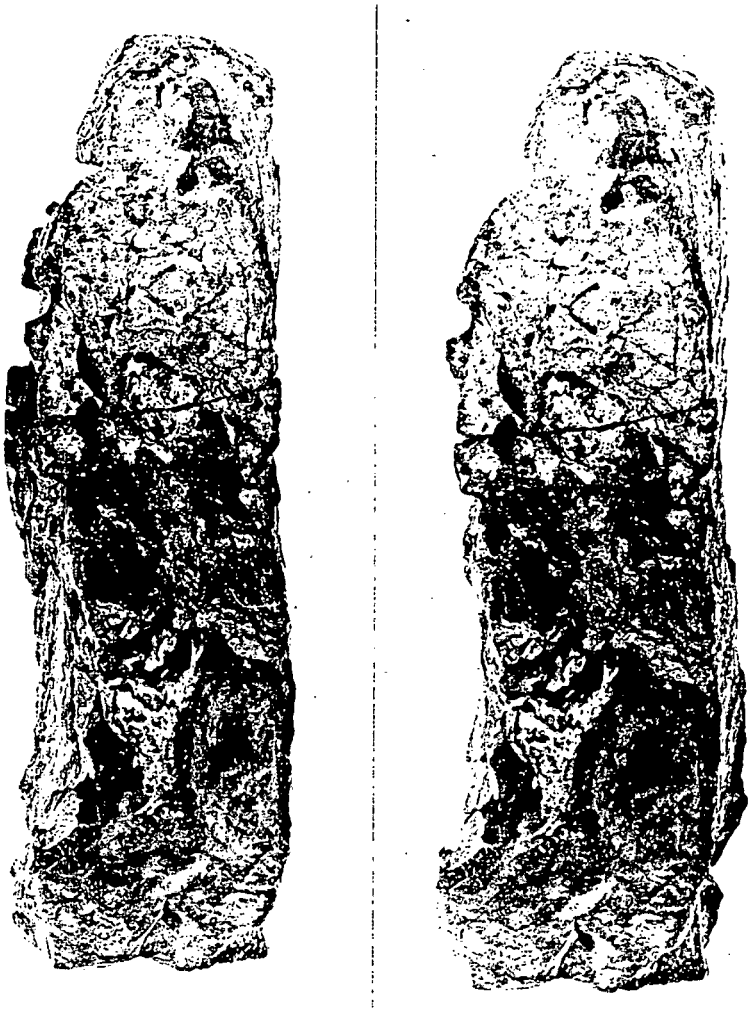

Fig. 75c Stereophotograph of the type skull of *Scylacosaurus sclateri* SAM 634. Left lateral view. Scale 20mm.

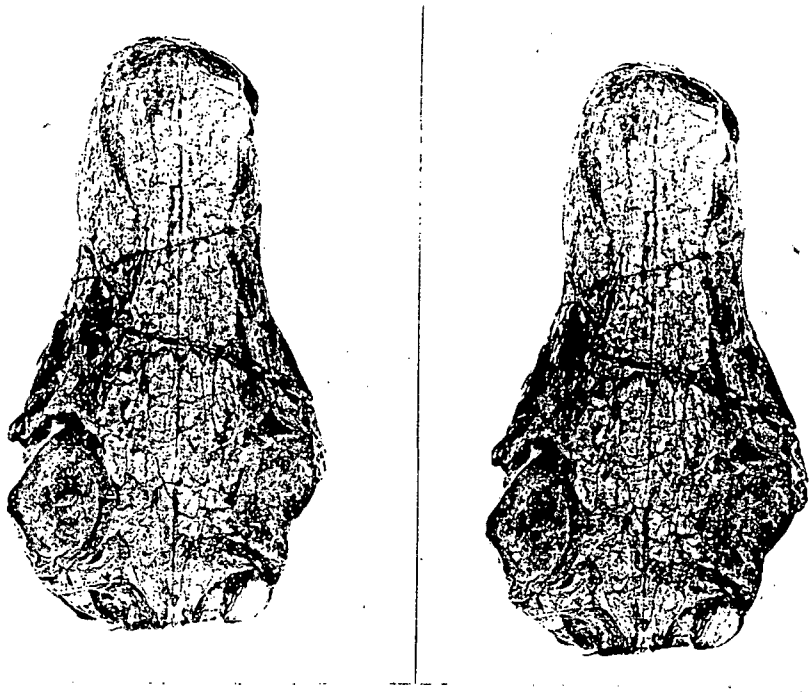

Fig. 75d Stereophotograph of the type skull of *Scylacosaurus sclateri* SAM 634. Dorsal view. Scale 20mm.

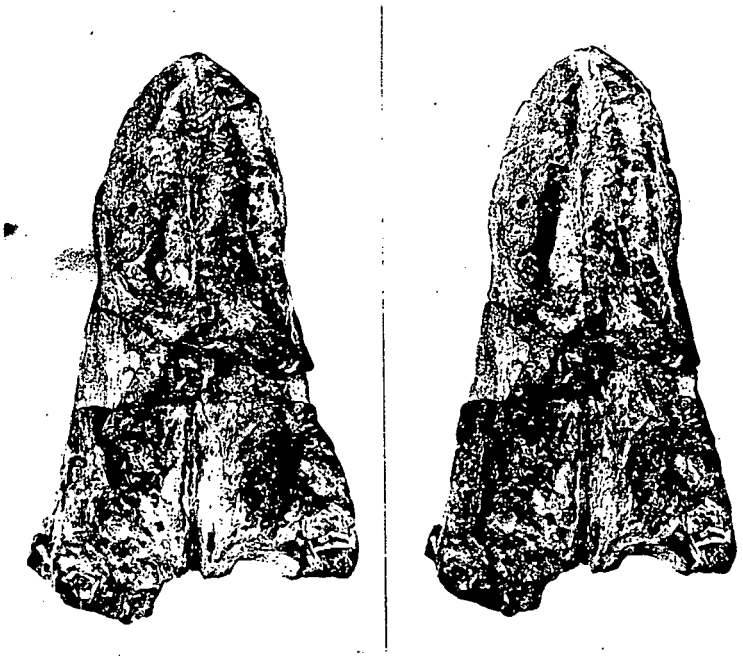

Fig. 76a Stereophotograph of *Scylacosaurus sclateri* AMNH 5560.
Dorsal view of palate. Scale 20mm.

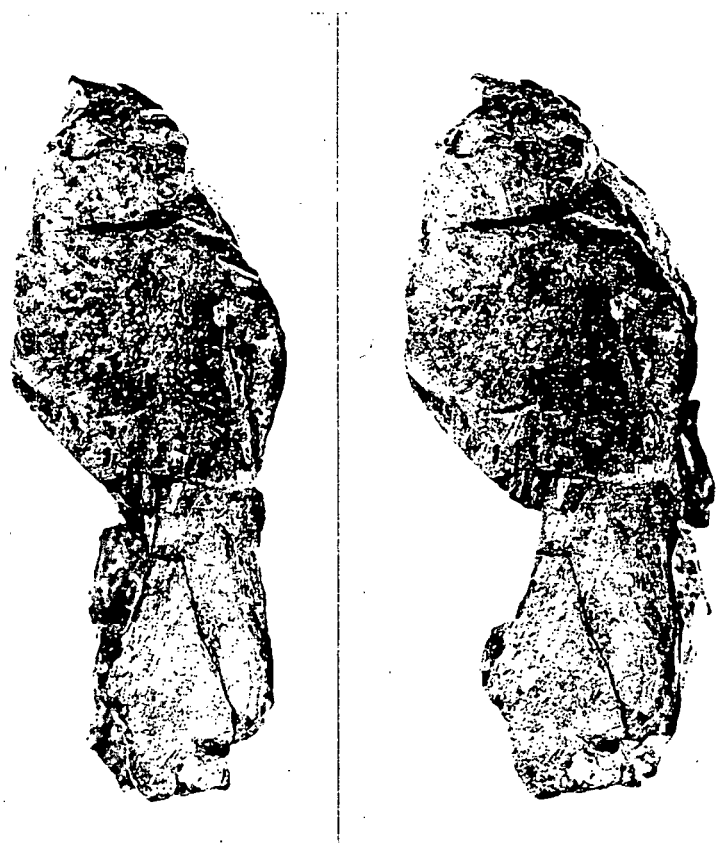

Fig. 76b Stereophotograph of *Scylacosaurus sclateri* AMNH 5560.
Right lateral view. Scale 20mm.

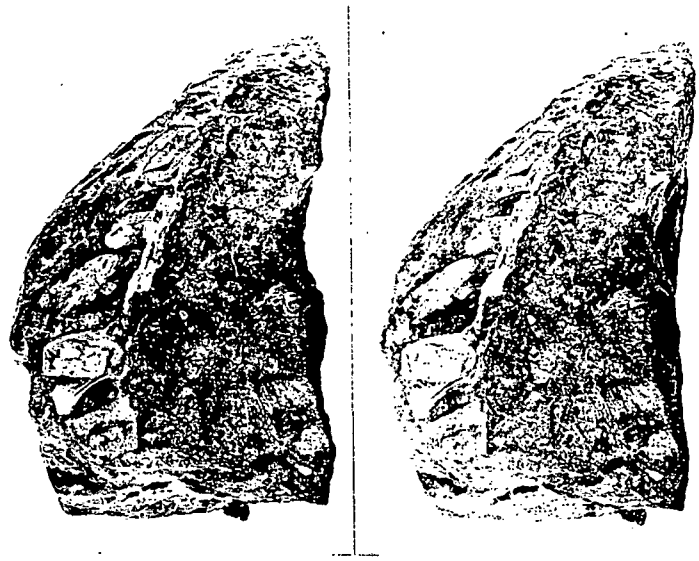

Fig. 77a Stereophotograph of the type of *Scymnosaurus ferox* SAM 632.
Left lateral view. Scale 20mm.

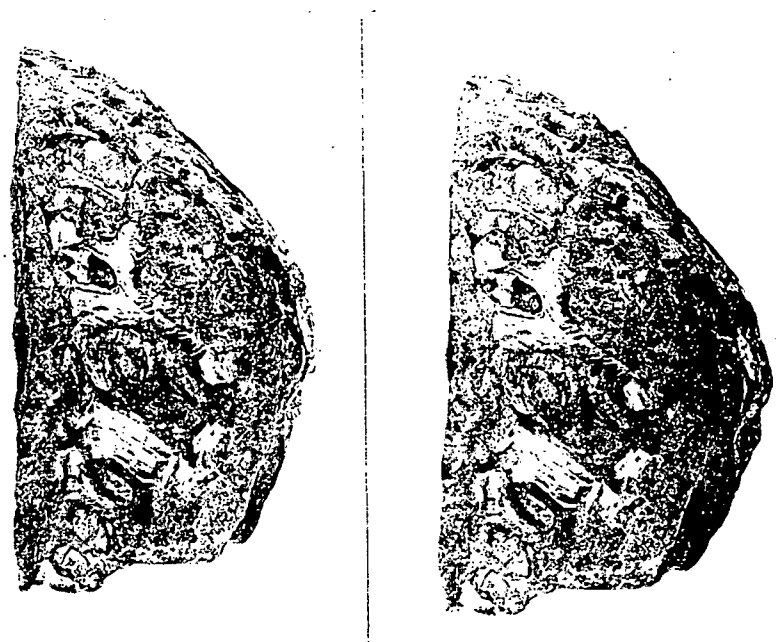

Fig. 77b Stereophotograph of the type of *Scymnosaurus ferox* SAM 632.
Right lateral view. Scale 20mm.

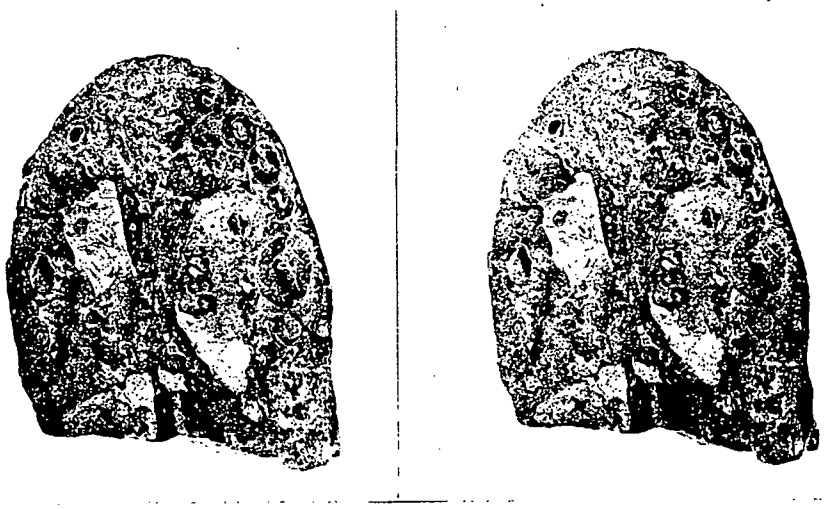

Fig. 77c Stereophotograph of the type of *Scymnosaurus ferox* SAM 632.
Dorsal view. Scale 20mm.

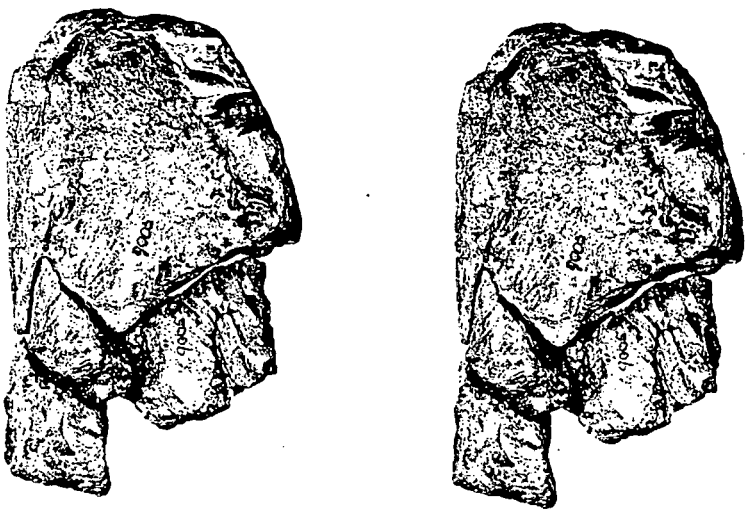

Fig. 78a Stereophotograph of the type of *Scymnosaurus major* SAM 9005
Right lateral view. Scale 20mm.

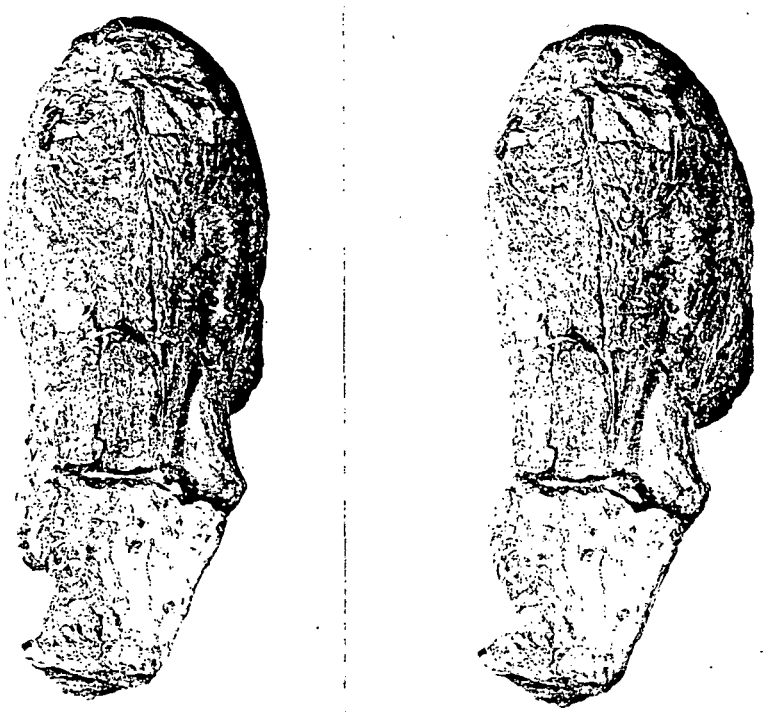

Fig. 78b Stereophotograph of the type of *Scymnosaurus major* SAM 9005.
Dorsal view. Scale 20mm.

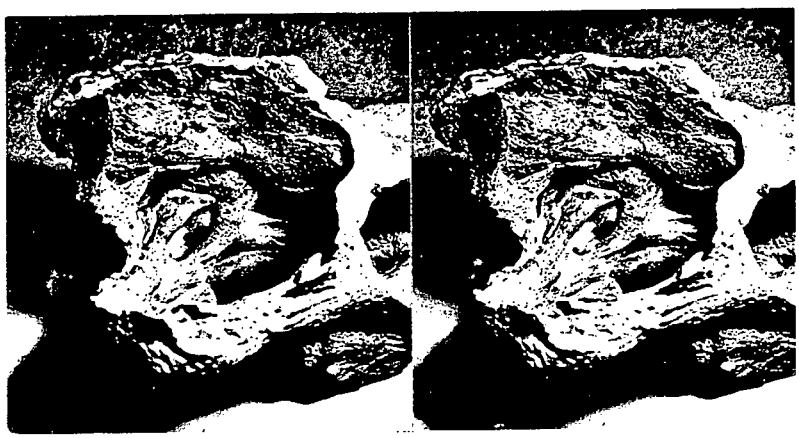

Fig. 79 Stereophotograph of the type of *Scymnosaurus watsoni* BMNH R4100. Right dorsolateral view of posterior half of skull. Scale 20mm.

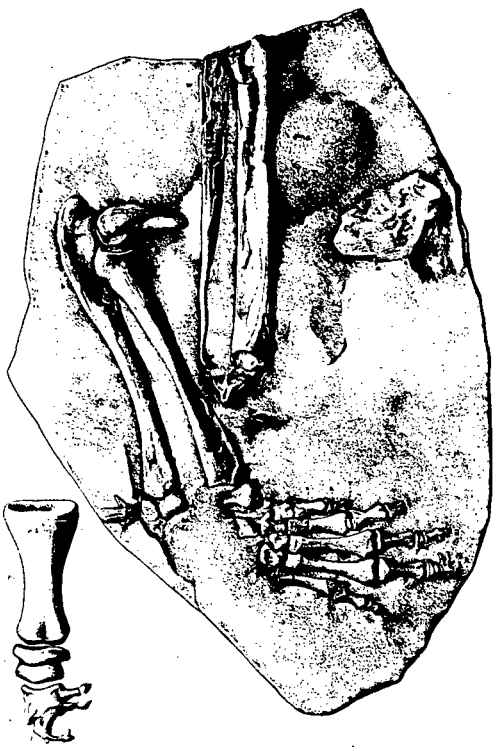

Fig. 80 Type of *Theriodesmus phylarchus* BMNH 49392. Scale 20mm.

(from Seeley, 1888)

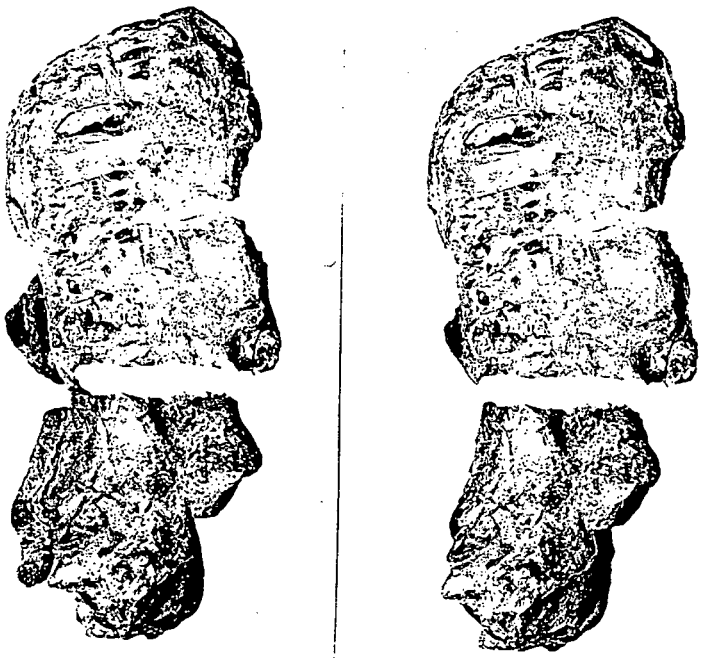

Fig. 81a Stereophotograph of the type skull of *Therioides cyniscus* SAM 11888. Left lateral view. Scale 20mm.

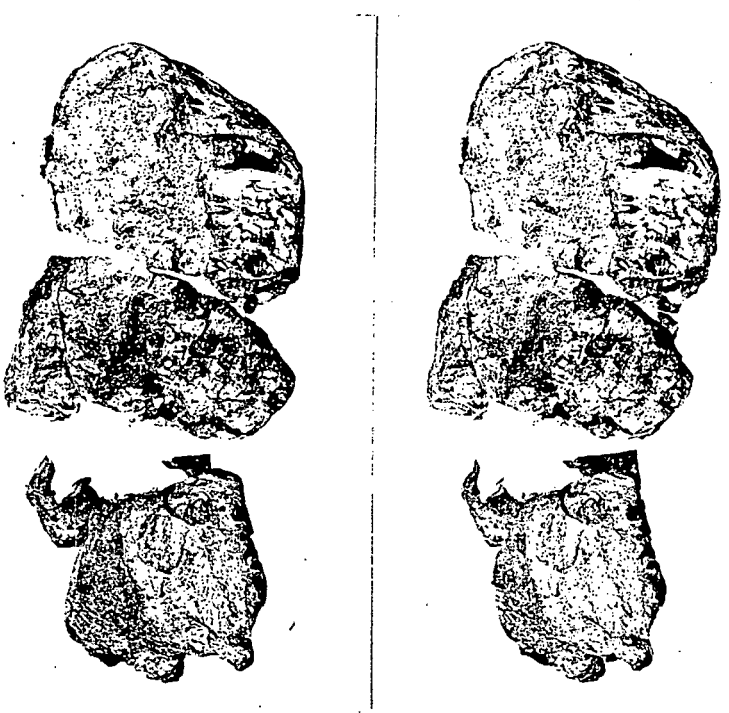

Fig. 81b Stereophotograph of the type skull of *Therioides cyniscus* SAM 11888. Right lateral view. Scale 20mm.

Fig. 81c Stereophotograph of the type skull of *Therioides cyniscus* SAM 11888. Close-up of left canine region. Scale 20mm.

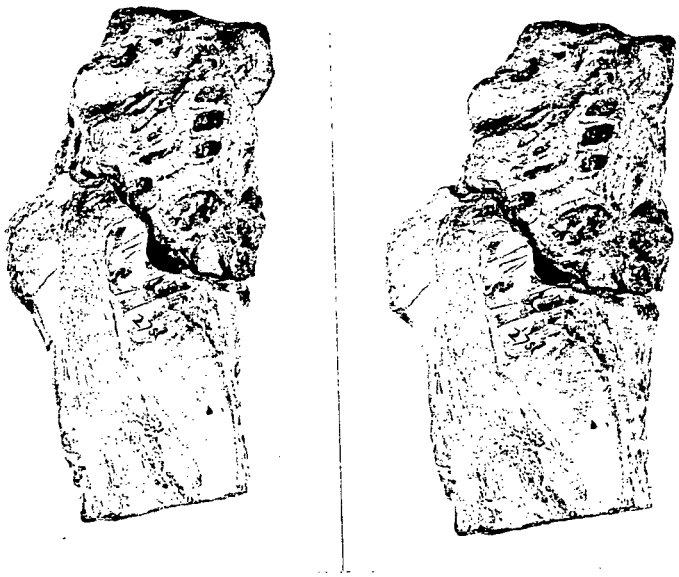

Fig. 82a Stereophotograph of the type of *Trochorhinus vanhoepeni* TM 275. Left ventrolateral view. Scale 20mm.

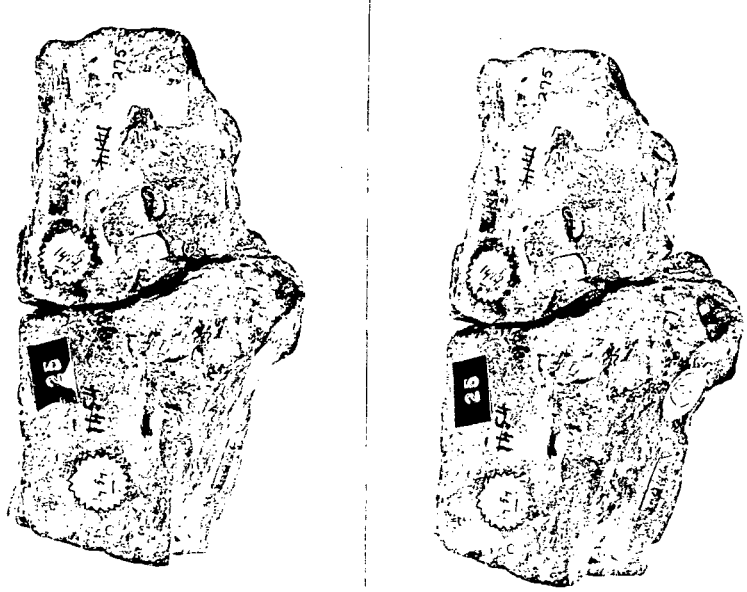

Fig. 82b Stereophotograph of the type of *Trochorhinus vanhoepeni* TM 275. Right lateral view. Scale 20mm.

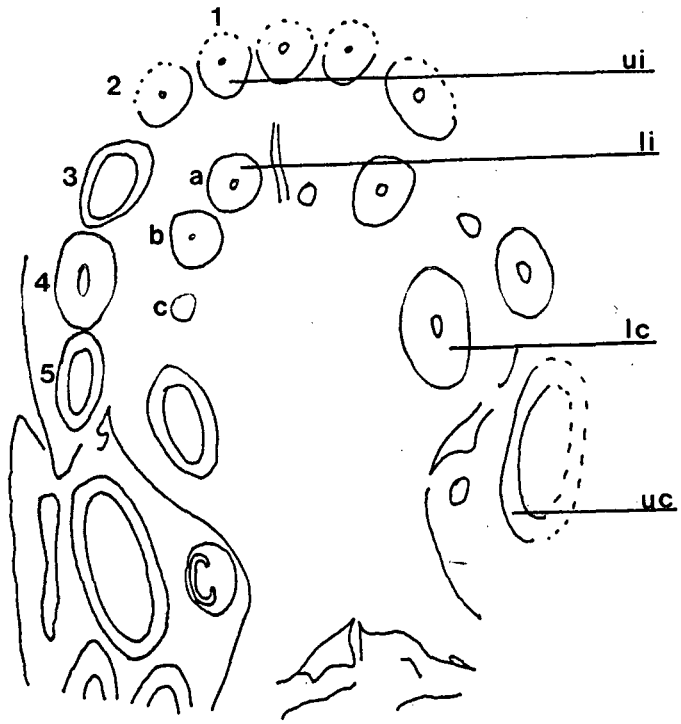

Fig. 83a Horizontal section through snout of *Trochosaurus dirus*. Scale 20mm. After Broom (1936c) Plate 1, Fig. 1.

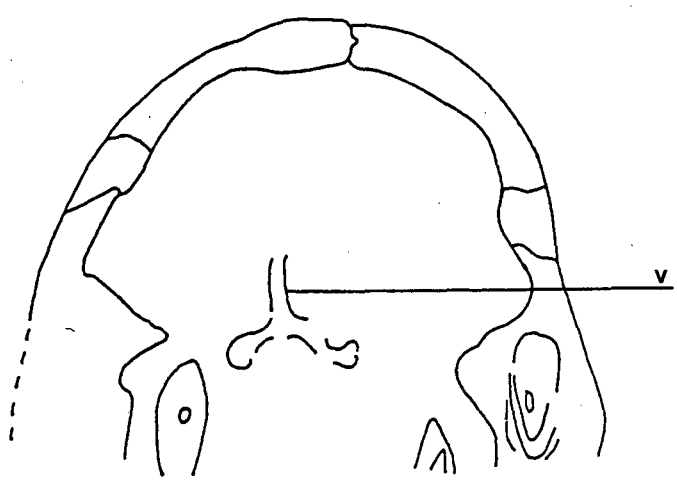

Fig. 83b Transverse section through anterior part of snout of *Trochosaurus dirus*. Scale 20mm. After Broom (1936c) Plate 1, Fig. 7.

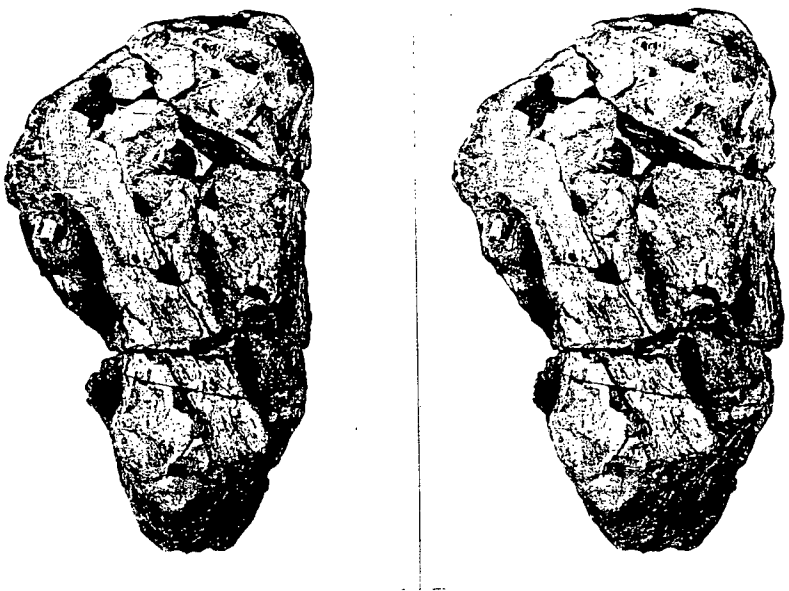

Fig. 84a Stereophotograph of the referred specimen of *Trochosaurus major (intermedius)* SAM 2756. Left lateral view. Scale 20mm.

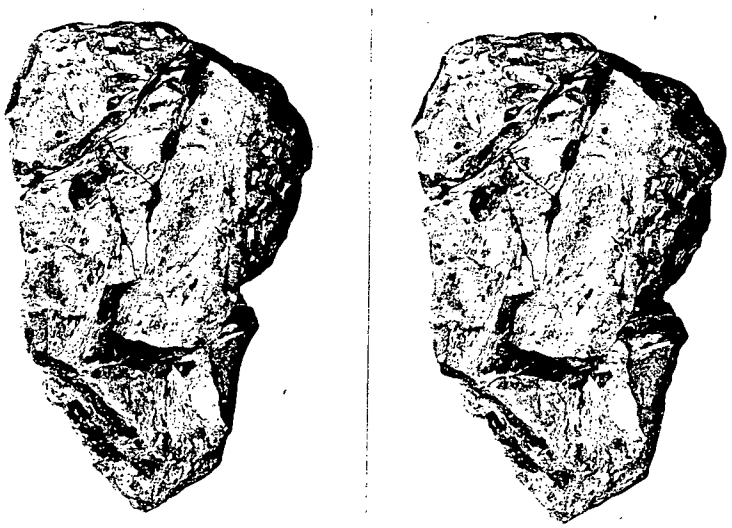

Fig. 84b Stereophotograph of the referred specimen of *Trochosaurus major (intermedius)* SAM 2756. Right lateral view. Scale 20mm.

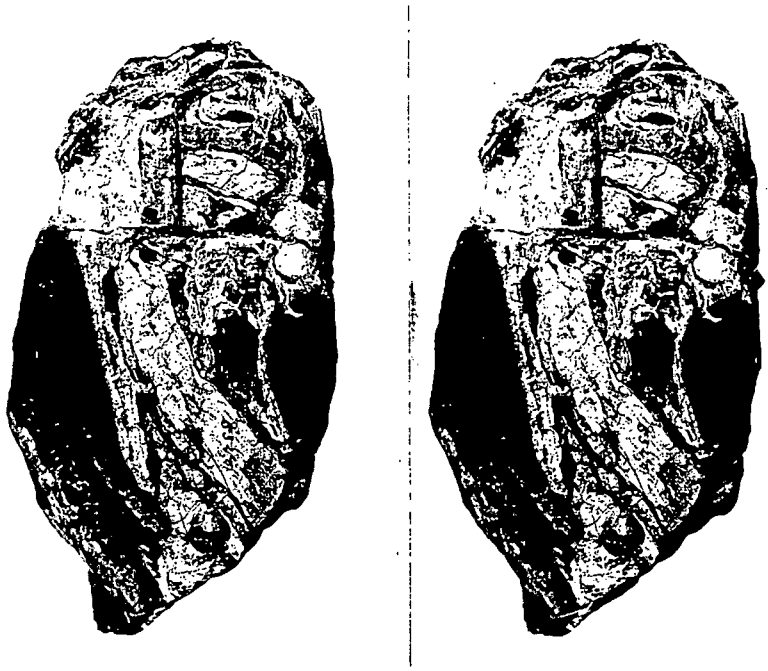

Fig. 85a Stereophotograph of the type of *Trochosaurus major* AMNH 5543. Left lateral view. Scale 20mm.

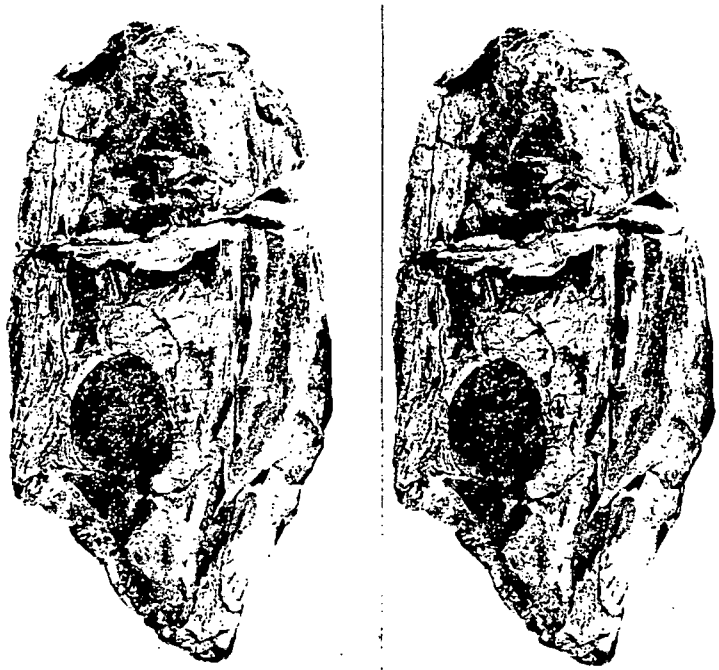

Fig. 85b Stereophotograph of the type of *Trochosaurus major* AMNH 5543. Right lateral view. Scale 20mm.

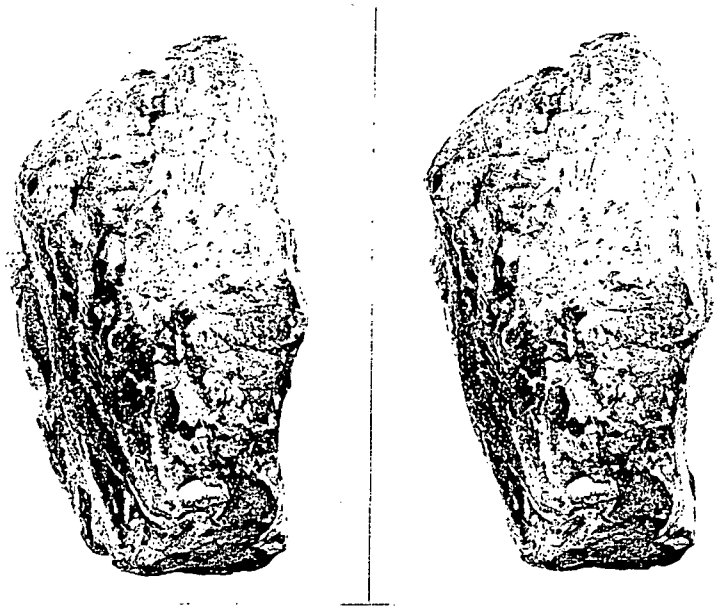

Fig. 86a Stereophotograph of the type of *Trochosuchus acutus* SAM 1076. Left lateral view. Scale 20mm.

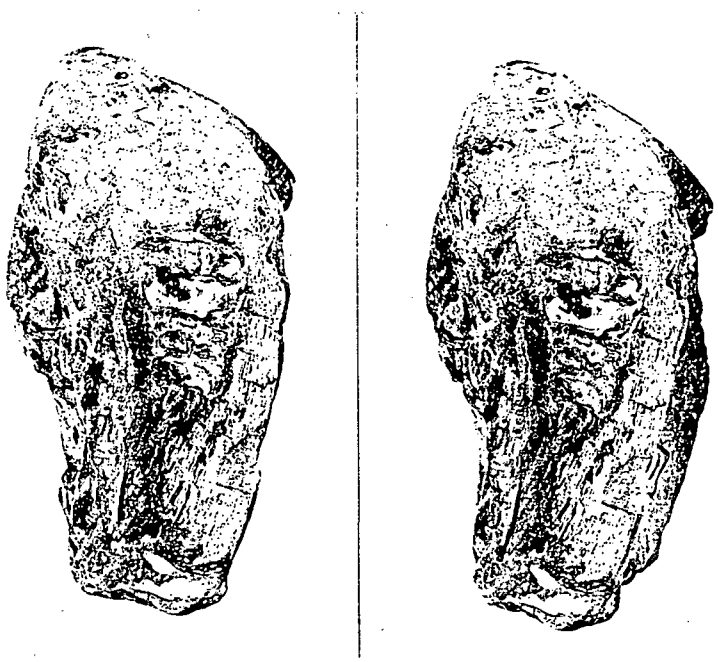

Fig. 86b Stereophotograph of the type of *Trochosuchus acutus* SAM 1076. Right lateral view. Scale 20mm.

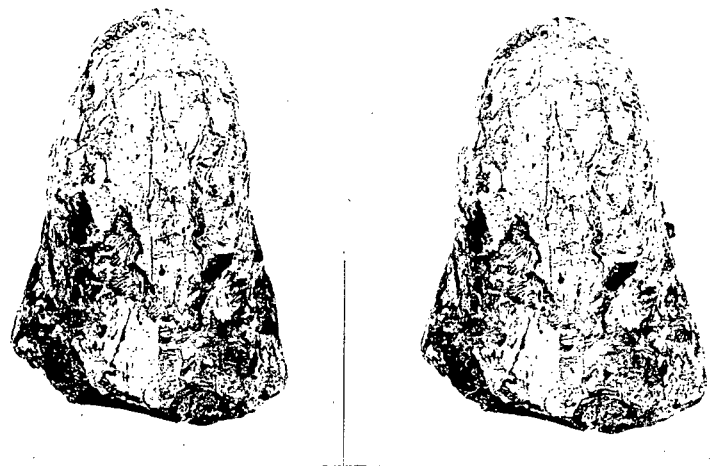

Fig. 86c Stereophotograph of the type of *Trochosuchus acutus* SAM 1076.

Dorsal view. Scale 20mm.

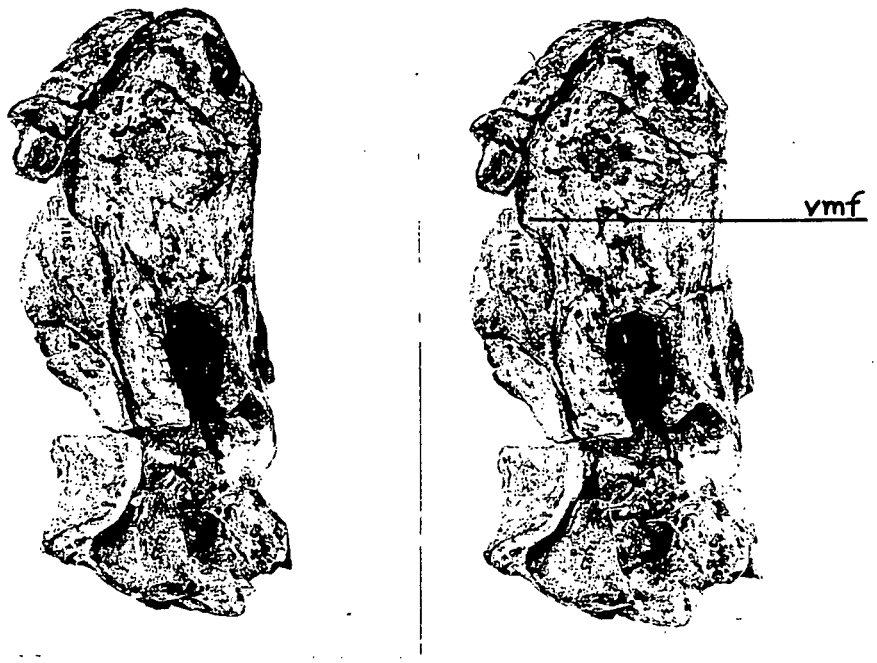

Fig. 87a Stereophotograph of the type of *Zinnosaurus paucidens* SAM 12185. Left lateral view. Scale 20mm.

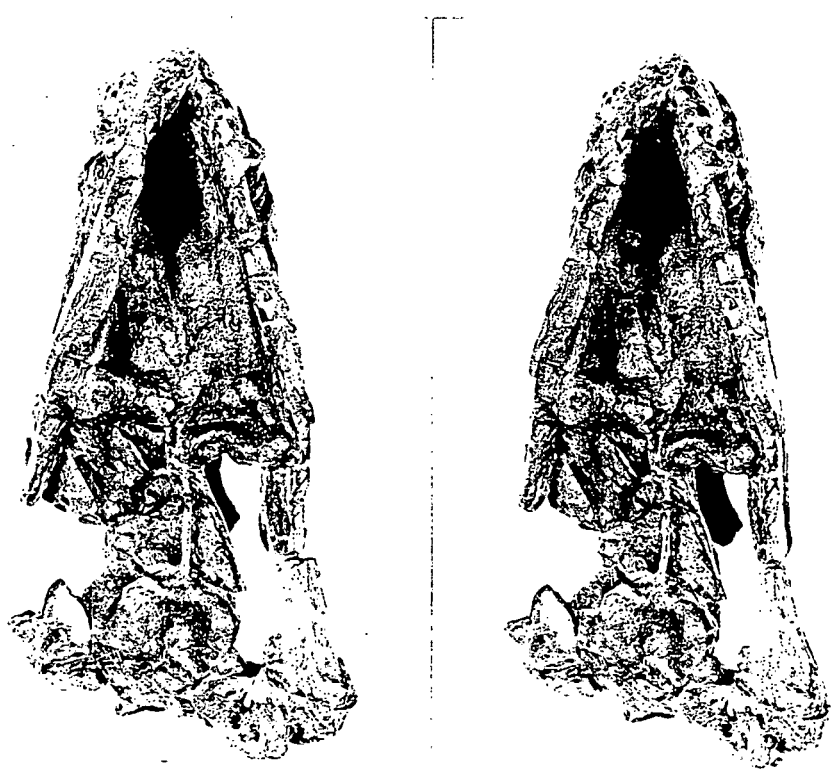

Fig. 87b Stereophotograph of the type of *Zinnosaurus paucidens* SAM 12185. Ventral view. Scale 20mm.

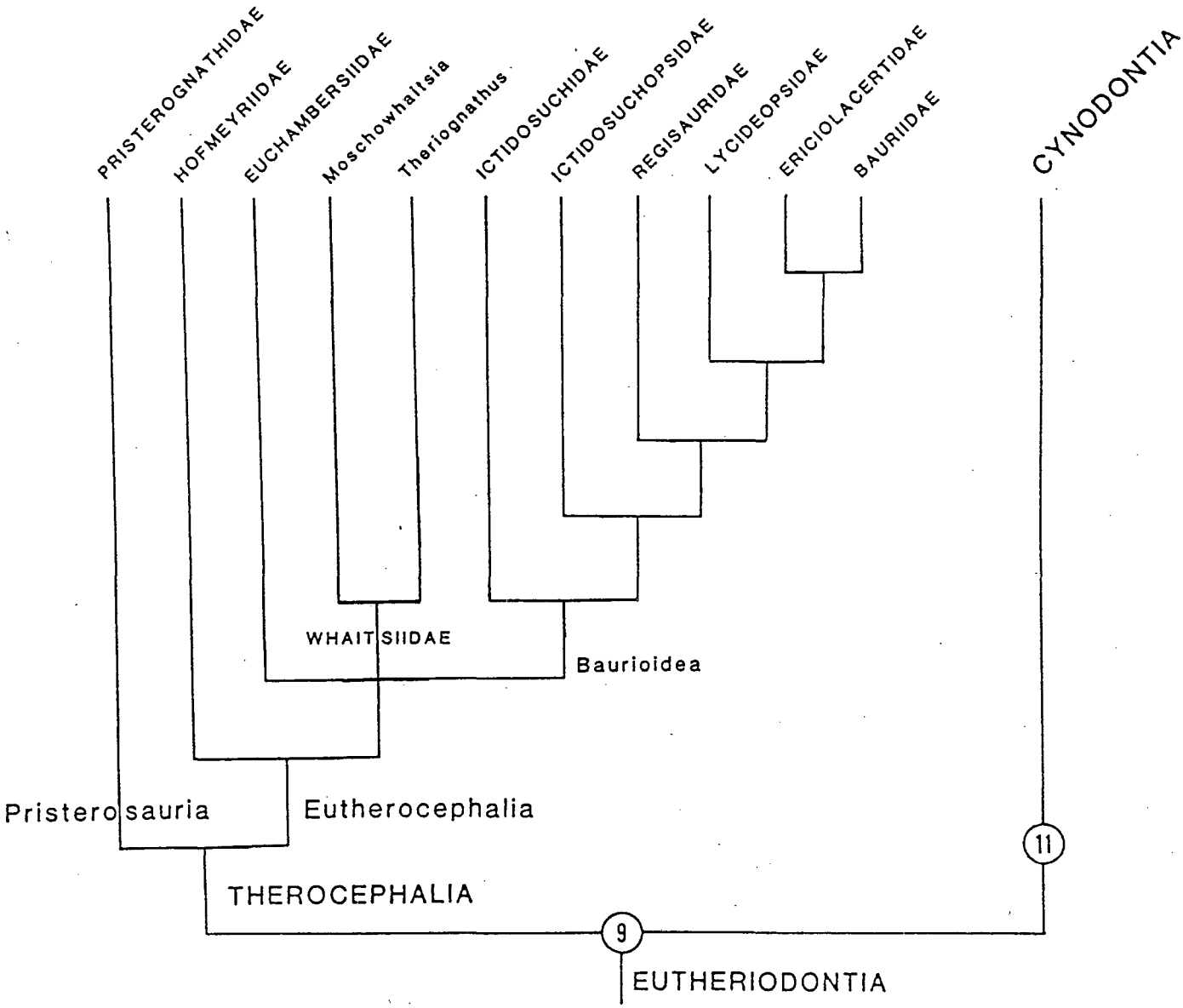

Fig. 88 Cladogram subdividing the Therocephalia according to Hopson & Barghusen (1986).

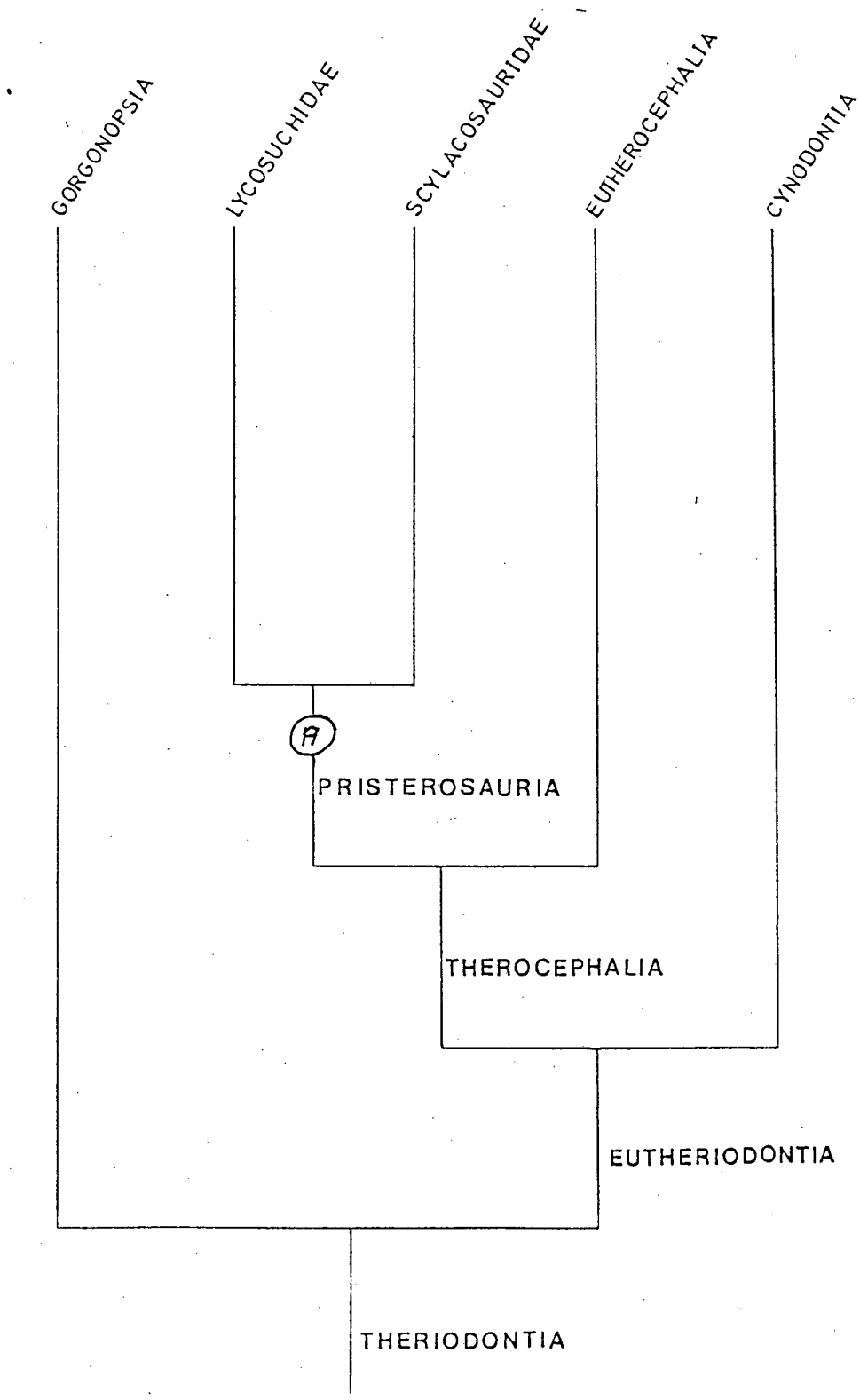

Fig. 89 Cladogram depicting the Pristerosauria (Lycosuchidae + Scylacosauridae) as the sister group of the Eutherocephalia.

A = Three mandibular incisors.

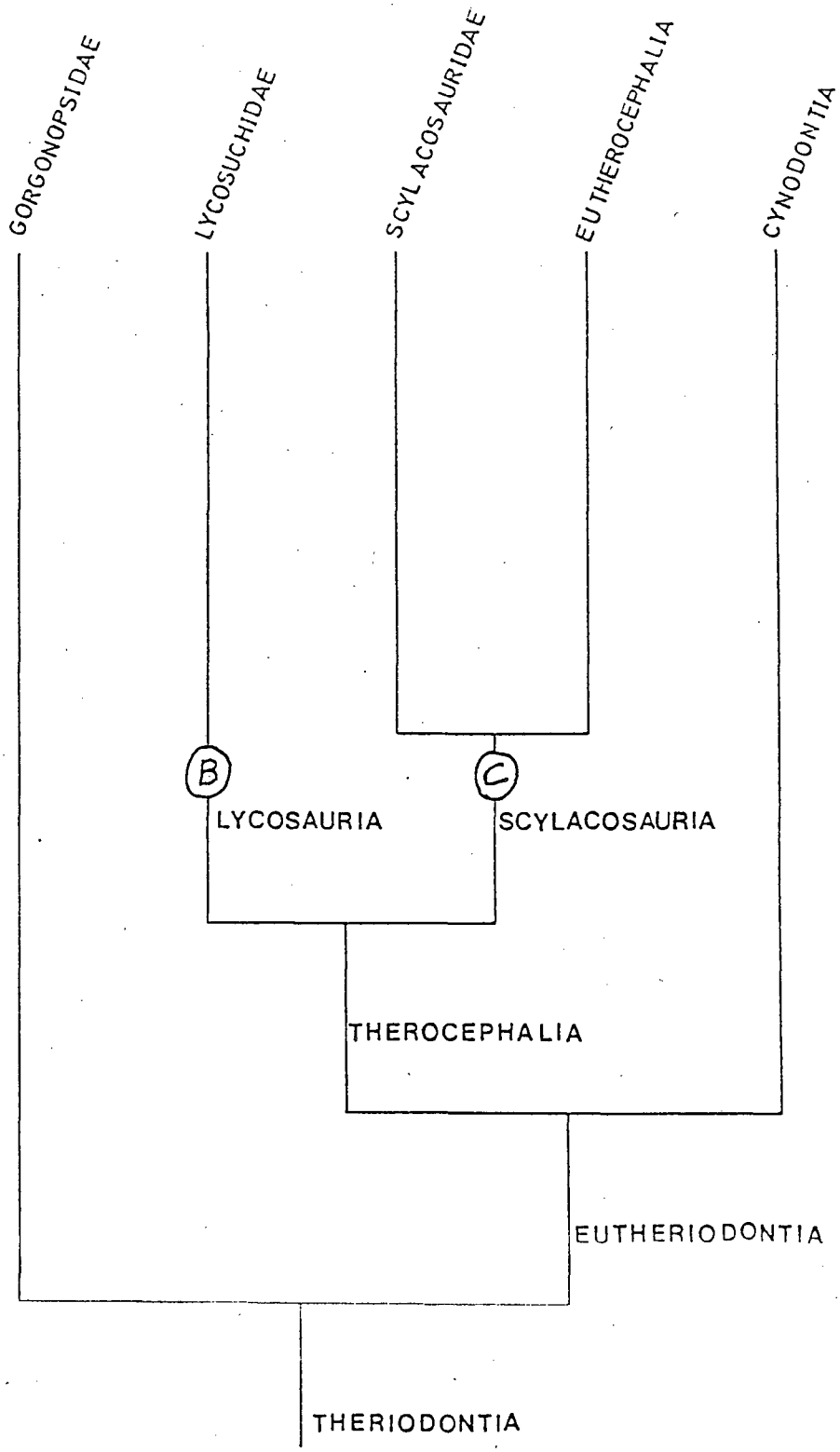

Fig. 90 Cladogram depicting the Lycosauria (Lycosuchidae) as the sister group of the Scylacosauria (Scylacosauridae + Eutherocephalia).

B = features 8, 10-14, 17, 19-20 and 23 as listed in text.

C = features 17, 19 and 23 as listed in text.

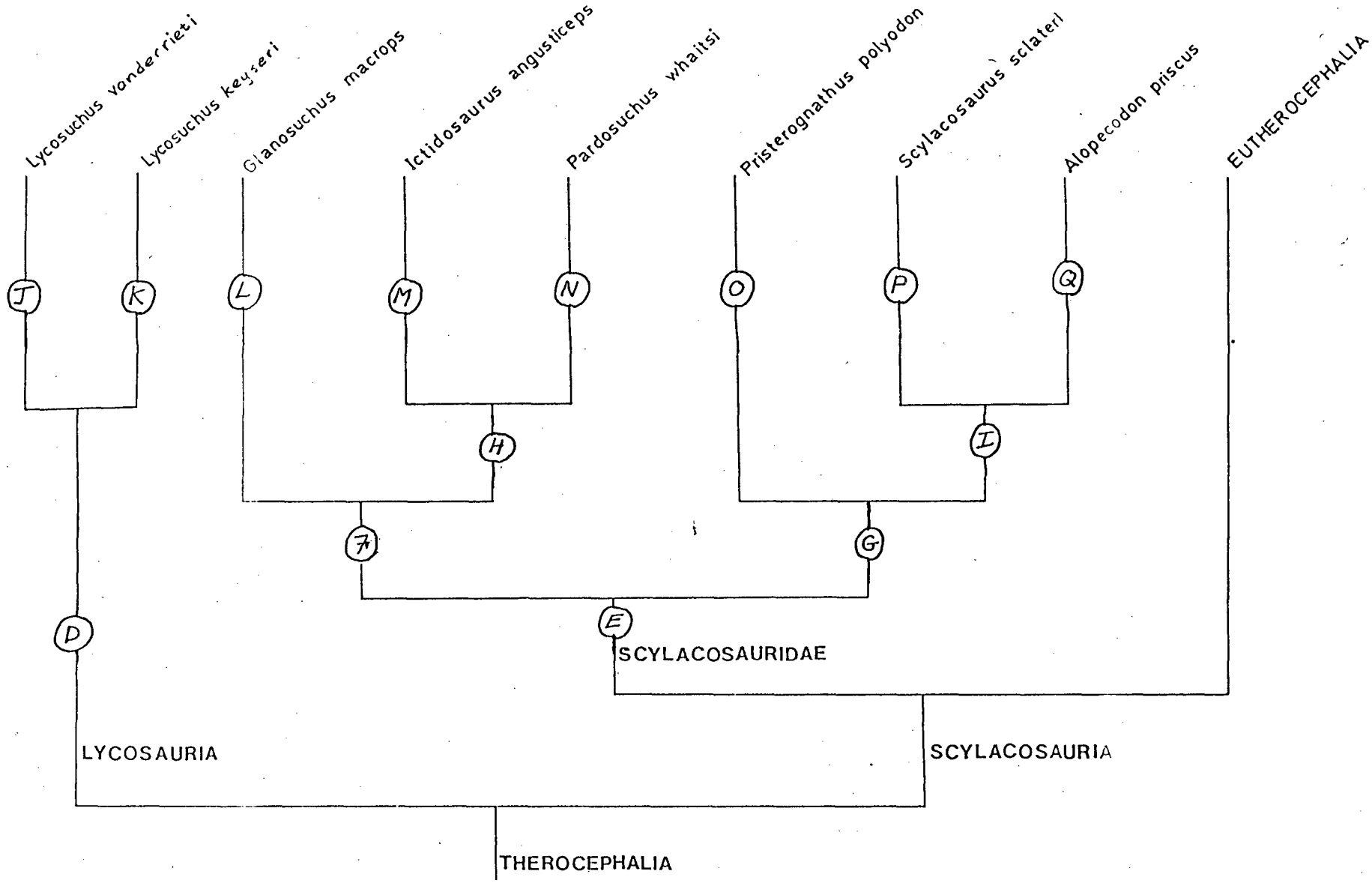

Fig. 91 Cladogram depicting subdivision of the Lycosauria and Scylacosauria. D = 5 upper incisors; E = 6-7 upper incisors, F = 6 upper incisors, G = 7 upper incisors, H + I = precanines present, J = ventral maxillary flange present, K = ventral maxillary flange absent, L + O = precannines lacking, M + P = 1 precannine present, N + Q = 2 precannines present.